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Fine-scale song exchange in two neighbouring populations of humpback whales

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Abstract

The songs of humpback whales (*Megaptera novaeagliae*), a patterned vocal display usually associated with breeding, serve as an excellent model of large-scale cultural transmission in a non-human species. These songs are considered to be particularly complex due to their well-known hierarchical structure and constantly changing nature. Two types of changes occur in the songs of the whales in the South Pacific meta-population: small, progressive evolutionary changes and radical cultural revolutions in which the song's pattern is entirely replaced during a single breeding season. While patterns of song change and the transmission of these changes among populations have been studied on a broad scale, fine-scale examination of the song's fundamental components (i.e. unit sequences) is lacking. This thesis aims to investigate fine-scale song structure in order to better understand song learning mechanisms. Firstly, intra-population song structures were examined within the east Australian song over time. Secondly, inter-population learning was assessed during the song's transmission to the neighbouring population that winters off New Caledonia.

Several quantitative methods were developed or applied here to identify song features at the unit sequence level. An acoustic dictionary of the song repertoire was created using a self-organising map, which quantified similarity between units and provided a robust means of classifying units. Metrics for measuring song complexity were modified to address the unique hierarchical structure of humpback whale song and quantify complexity at multiple levels in the song. An analysis of network structure, previously only applied to human language and birdsong, was used to measure the connectivity of units within song arrangements. These methods were applied to the transcription of songs over 13 consecutive years in east Australia and two consecutive years with two song types in New Caledonia, allowing for fine-scale features to be described and quantified.

To understand song learning within a single population, fine-scale structural features of the east Australian song were quantified over the same period. The complexity of both theme and unit sequences fluctuated over time, showing a clear relationship with both progressive, evolutionary changes and revolutionary events. Songs became increasingly more complex as the songs evolved through small additions of novel material, but were simplified when cultural revolutions replaced the song pattern. However, these fluctuations were not reflected in underlying network structures or second order entropy of each song. Every song displayed a degree of "small-world" network structure characterised by clusters of highly connected units. Additionally, they contained fine-

scale structures such as deterministic transition patterns (i.e. doublet and triplet repetitions), redundant unit usage, and predictable unit arrangements. These features were always present despite marked differences in songs from year to year and are likely to facilitate song learning.

How structural features changed during transmission between east Australia and New Caledonia provided insight into inter-population social learning. Each individual theme maintained or increased its complexity during transmission, but the song's arrangements and the underlying small-world structure remained largely unchanged. Songs were therefore learned across populations with high fidelity and without needing to be simplified. Such precision probably requires a mechanism of song transmission with a high degree of acoustic contact. Recent studies have suggested that such acoustic contact may occur on the shared Antarctic feeding grounds or individual movement between populations.

This thesis is the first study to quantify the fine-scale structural and syntactic features of humpback whale song, and does so over multiple years and across two adjacent populations. These results indicate that song learning is probably influenced by a combination of conformity to an underlying structural template and small individual additions of novel material that increase complexity in the song's arrangement. Widespread rules of song structure should be explored in future studies by examining these fine-scale song features in other populations or ocean basins.

Features identified here such as small-world networks and central 'hub' units also occur in other complex vocal learning displays, such as birdsong and human language. These commonalities suggest a convergence of certain features in vocal learning across multiple taxa. Given how integral social learning is within human evolution and culture, comparative information on social learning across non-human species is a key factor in further understanding our own cultural evolution.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, financial support and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my higher degree by research candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

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Publications during candidature

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This thesis used adult male humpback whales from the east Australia and New Caledonia populations as subjects. Animals were recorded using passive acoustic recorders or boat-based hydrophones.

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Please find copies of all ethics approval certificates in Appendix 5

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List of Abbreviations

Behavioural Responses of Australian Humpback whales to Seismic Surveys (BRAHSS)

Classification and Regression Trees (CART)

Contoured (C)

Cophenetic correlation coefficient (CCC)

Discriminant function analysis (DFA)

Fast Fourier Transform (FFT)

Humpback whale Acoustic Research Collaboration (HARC)

Levenshtein distance analysis (LDA)

Levenshtein Similarity Index (LSI)

Non-contoured (NC)

Out-of-bag error rate (OOB)

Principal component analysis (PCA)

Pulse repetition rate (PRR)

Qualitative (Q)

Self-Organizing Map (SOM

Signal-to-noise ratio (SNR)

CHAPTER 1 Introduction and Literature Review

1.1 Thesis overview and aims

The songs of humpback whales (*Megaptera novaeangliae*) are an excellent model of large-scale cultural transmission in a non-human animal (Noad *et al.*, 2000; Rendell and Whitehead, 2001; Garland *et al.*, 2011; Whitehead and Rendell, 2014). Song, a patterned vocal display usually associated with breeding, is a phenomenon found throughout the animal kingdom (Catchpole and Slater, 2008; Koren *et al.*, 2008; Kershenbaum *et al.*, 2014a). In many species, there are syntactic rules that govern the song's structure or arrangement (Marler, 1977; Berwick *et al.*, 2011; Kershenbaum *et al.*, 2014a). Humpback whale song is a particularly complex display due to its hierarchical structure and constantly changing nature (Payne and McVay, 1971; Payne *et al.*, 1983). Both small 'evolutionary' (Payne *et al.*, 1983; Garland *et al.*, 2011) and large 'revolutionary' changes (Noad *et al.*, 2000; Garland *et al.*, 2011) can occur within the song. While patterns in these changes have been studied on a broader scale (Garland *et al.*, 2011), few studies have examined them at a fine scale (Payne *et al.*, 1983; Green *et al.*, 2011; Garland *et al.*, 2017a; Murray *et al.*, 2018). My thesis focuses on the fine scale patterns in structure and syntax that occur in the east Australian song as it changes from year to year, and as the song passes to the neighbouring population that winters off New Caledonia through population-wide social learning. Consistent patterns at the fine scale level would indicate what types of rules humpback whales might follow when learning their song, which may in turn make the song itself easier to learn.

My thesis will determine if humpback whale song follows a specific set of syntactic or structural rules and how this influences the cultural learning of their songs. After an initial methods chapter which will quantitatively categorise signals in the song repertoire (chapter 2), each of the data chapters will look at structural patterns on a different scale: within the changes in song complexity levels in one population over time (chapter 3), within the syntax and network structure of one population over time (chapter 4), and within multiple populations that transfer the song between them (chapter 5). The patterns or rules found could provide insight into the function or meaning of the song display, which is still debated. Any consistent patterns or features could be compared to those found in the vocal learning displays of other species. Shared structural features or syntactic rules would indicate potentially shared features of vocal learning across species. Given how integral social learning is to the evolution of human language and culture, comparative information on social learning among non-human species is a key factor in further understanding our own cultural traits.

1.2 Culture and social learning

The study of culture is well established in humans, but its application to animals has long been debated. Much of this results from the inability of the scientific community to settle on a single objective definition for the term 'culture'. Often the definitions use a subjective set of criteria, making it difficult to form a consensus on its applied meaning. Rendell and Whitehead (2001) summarised these definitions, ranging from "behavioural variants induced by social modification, creating individuals who will in turn modify the behaviour of others" (Kummer, 1971) to "shared ideational phenomena (ideas, beliefs, values, knowledge)" (Feldman and Laland, 1996). When it comes to animal culture, there are at least a few shared concepts within the various definitions of a cultural behaviour (Rendell and Whitehead, 2001; McGrew, 2009):

1. It is learned rather than a trait that develops instinctively or without social input
2. It is considered normative (i.e., driven by social interaction) within the group or population
3. It is collective among all the individuals that acquire it
4. The mechanism of transfer is social, rather than asocial such as trial and error.

For the context of this study, culture is defined based on Rendell and Whitehead (2001) and Laland and Janik (2006) as a shared behaviour transmitted between conspecifics through social learning.

Social learning itself can come in several forms. Vertical transmission occurs from parent to offspring, making it difficult to distinguish from genetically determined traits (Cavalli-Sforza, 1981). The sponging foraging strategy of bottlenose dolphins (*Tursiops truncatus*) in Shark Bay, Western Australia is an example of this. While sponging occurs in a single matriline, it does not coincide with any simple genetic mechanisms of inheritance (Krützen *et al.*, 2005; Kopps and Sherwin, 2012). Oblique transmission occurs when a behaviour moves to an individual from a non-parental conspecific belonging to a previous generation, such as aunts, uncles, or unrelated teachers (Cavalli-Sforza, 1981). This is the dominant form of cultural transmission in song learning among bird species in which young males tend to learn from neighbouring older males (Cavalli-Sforza, 1981; Lachlan and Servedio, 2004; Catchpole and Slater, 2008). Horizontal transmission occurs through peer-to-peer exchange between individuals from the same generation. Examples can most readily be seen in the regional dialects of certain songbirds (Slater, 1986) and a variety of foraging and tool use behaviours in primates (Whiten *et al.*, 1999). Social transmission processes involve an observer-demonstrator dynamic that usually come in the form of 1) imitative or observational learning, 2) facilitation of the target behaviour, or 3) potential instances of direct teaching (Guinet and Bouvier, 1995; Hoppitt and Laland, 2008).

Cultural transmission was thought to be uniquely human because we rely on it to a degree far beyond that of any other species. The accumulation of knowledge with each passing generation has become so vast and intricate that there is no other realistic method for us to learn what we need for success (Laland, 2004). Which species and which behaviours have an affinity for social transmission depend upon a number of factors. Socially tolerant species are more likely to engage in social learning than solitary ones because there is more individual-level interaction and group cohesion (Coussi-Korbel and Fragaszy, 1995; Sargeant and Mann, 2009), thus presenting more opportunity for individuals to acquire information from one another. Direct contact with the environment makes asocially learned information more reliable while social learning is often indirect (Rogers, 1988; Giraldeau *et al.*, 2002; Laland, 2004). However, social learning is less costly because not all individuals need to expend resources acquiring information from the environment (Laland, 2004).

Fitness costs play an important role in social learning compared to asocial mechanisms, such as trial and error, because they affect both the individual and the group as a whole (Boyd and Richerson, 1988b; Feldman *et al.*, 1996; Laland, 2004). For example, individuals often do not have to spend as much time and effort learning a trait socially and can subsequently pass it on more quickly (Laland, 2004). Other costs could be incurred due to risks such as the possibility of acquiring inaccurate information or the negative consequences of being unable to learn (Boyd and Richerson, 1988a). Sometimes cost might be weighed against how productive the behaviour is; other times cost refers to the effort of transmitting the behaviour to a naïve individual (Laland, 2004). Transmission can occur directly when the identity of both the informed and naïve individuals influence the learning rate. It can also be non-specific, meaning that any two individuals can learn from one another. Proximity and behavioural coordination in either time or space can allow those with weaker social structures to socially transmit information (Coussi-Korbel and Fragaszy, 1995). Often additional external variables such as environmental conditions or the adaptive value of the behaviour will affect how significant the influence of social learning is. Interactions between all of these factors results in a gradient on which different types of social transmission occur. Some behaviours transmit only to a few individuals while others become widespread through the entire population (Sargeant and Mann, 2009).

Culture, defined here as behaviour shared by social learning, occurs in a wide variety of animals from rats (Terkel, 1996) to coral reef fish (Warner, 1988) to lemurs (Kendal *et al.*, 2010).

However, much of the evidence lies within three main groups: songbirds, primates, and cetaceans (Rendell and Whitehead, 2001). Some of the first documented examples of non-human culture came from primate studies of foraging strategies such as the spread of sweet potato washing in Japanese macaques (*Macaca fuscata)* (Kawai, 1965) or the multiple uses of tools in chimpanzees (*Pan troglodytes*) (Whiten *et al.*, 1999). Foraging behaviours lend themselves to social transmission because both phenomena are closely tied to individual and group fitness (Laland, 2004). As previously discussed, the cost of a strategy and its productive value are significant factors in whether social learning is employed. The costs and benefits of foraging techniques often impact fitness level more substantially than other types of behaviours, leading social learning to play an important role in their development and use (Sargeant and Mann, 2009). Behaviours that serve a purely social function such as bond strengthening often transfer socially. This is more common in animals with strong social cohesion, such as monkeys, which have traditions meant to encourage community bonding (Perry and Manson, 2003).

1.3 Vocal learning and communication

Vocal learning and communication provide much of the literature on non-human culture (Laland and Janik, 2006). Extensive concentration in this area has been on song dialects and the vocal communication seen in avian and mammalian species. In the last few decades, this has expanded to include cetaceans. Vocal signals serve diverse functions within a species. Most bird species use songs (patterned vocalisations) as a means of sexual selection, territorial claims, and to establish social hierarchy (Catchpole and Slater, 2008). Primate vocal signals have a high amount of plasticity in their call types and usage (Snowdon, 2009). Rough calls in chimpanzees indicate what types of food are found while foraging (Slocombe and Zuberbühler, 2006). Diana monkeys (*Cercopithecus diana*) raise specific alarms to differentiate between types of predators (Zuberbühler *et al.*, 1999). Primates can also use vocal signals to convey social structure, as seen in the 'wahoo' calls of male baboons (*Papio cynocephalus ursinus*) which indicate their quality or status (Fischer *et al.*, 2004).

Cetaceans also use vocalizations in a wide range of contexts, largely because of their dependence on sound. Odontocetes use echolocation to navigate through their environment and to forage (Herman and Tavolga, 1980; Au *et al.*, 2013). Signature whistles in bottlenose dolphins identify both themselves and other individuals they associate with (Janik *et al.*, 2006). Killer whale (*Orcinus orca*) pods group into distinct acoustic clans with culturally transmitted dialects through maternal lineages (Yurk *et al.*, 2002). While mysticetes do not use echolocation, they do make a

number of vocal calls or signals. Many baleen species produce songs with varying degrees of complexity, including blue (*Balaenoptera musculus*), fin (*Balaenoptera physalus*), humpback, and bowhead whales (*Balaena mysticetus*) (McDonald *et al.*, 2006; Širović *et al.*, 2007; Delarue *et al.*, 2009). Other types of calls occur in social, sexual or foraging situations. Examples include the gunshot calls of right whales (*Eubalaena glacialis*) as a potential reproductive advertisement (Parks *et al.*, 2005), social sounds made by humpback whales while in social groupings (Dunlop *et al.*, 2007), or the downsweep D-calls of blue whales during foraging (Oleson *et al.*, 2007).

Living in the marine environment adds a unique dimension to communication because of how differently sound propagates in water. An acoustic signal underwater will travel effectively over a greater distance than in air (Herman and Tavolga, 1980; Richardson *et al.*, 1995; Thomson, 1995). Combined with poor visibility, it results in the heavy reliance on aural cues observed in cetaceans. This reliance also means that how conspecifics interact differs from terrestrial species (Herman and Tavolga, 1980). The active space, or range within which a signal can reach potential receivers, is much bigger underwater than on land (Brenowitz, 1982). This makes interactions between conspecifics more complex. Determining the spatial range of low frequency signals with high intensity (e.g., the calls of blue and fin whales) and who those signals may be reaching is limited by methods of study and analysis (Širović *et al.*, 2007). This is one of the main obstacles in determining the function of acoustic communication in cetaceans.

Marine species face a distinctive set of communication issues due to their acoustic environment. Sound propagation makes the underwater environment a noisy place due to biological sounds, wind-driven sound at the surface, and geological events. Adding to this, anthropogenic noise pollution has increased dramatically in the past century with increases in industrial shipping, boat traffic, seismic exploration, and military activities such as sonar testing (Payne and Webb, 1971; Richardson *et al.*, 1995). Exposure to high acoustic levels can result in an increase in the threshold of hearing. This shift can be temporary in moderate cases or permanent in severe ones (Nowacek *et al.*, 2007). Extraneous sound can mask signals of the same frequency, which can reduce the active space of that signal and make it harder to detect (Brenowitz, 1982). Often animals will respond by adjusting their signal to compensate. Changes in acoustic characteristics such as the frequency, rate, duration, or amplitude occur in an effort to reduce degradation (Nowacek *et al.*, 2007). This is analogous to changing how one speaks in a crowded room. For instance, dolphins increase their whistle rate in the presence of boat traffic (Buckstaff, 2004), while right whales increase the amplitude of their calls when low frequency noise levels increase (Parks *et*

al., 2007). How this might affect the species themselves is largely dependent on the function of the impacted signals. From a conservation standpoint, this makes the potential consequences difficult to assess.

One major hurdle in the study of vocal communication is a means of quantitatively classifying signals. Although acoustic signal features such as duration or frequency can be measured (Tchernichovski *et al.*, 2000; Cerchio *et al.*, 2001), they do not always completely and accurately represent the signal (Janik, 1999). As a result, the signals in a display are often classified qualitatively by a human observer (Janik, 1999; Kershenbaum *et al.*, 2014a). The qualitative grouping of signals can be corroborated through a number of techniques. Naïve matching between observers is often used to determine if individuals will independently categorise the same signals in the same way. Multivariate statistics such as principal component analysis (PCA) or discriminant function analysis (DFA) were previously common tools, particularly for animal vocal displays (Boisseau, 2005; Dunlop *et al.*, 2007; Rekdahl *et al.*, 2013). However, these statistics require data to meet a number of assumptions. Variables must be parametric, normally distributed, uncorrelated, and independent. Few datasets meet such criteria, necessitating the use of alternative methods. Decision tree analyses such as classification and regression trees (CART) or random forest analysis allow data to violate the assumptions that PCA or DFA require (Van Opzeeland and Van Parijs, 2004; Melendez *et al.*, 2006; Garland *et al.*, 2012; Rekdahl *et al.*, 2013). However, none of these methods provides a way to make classification more objective – they can only validate previously made qualitative classifications. More quantitative means of classification, such as artificial neural networks like self-organizing maps (SOM) (Kohonen, 1990), are needed in order to make analyses of vocal displays more objective, robust, and repeatable.

Vocal learning usually comes in two forms: contextual or production. Contextual learning involves an existing signal utilised in a new context without changing the acoustic features. This type of learning occurs for two reasons: either the circumstances of a signal's use have been deliberately changed, or a random response to a new stimulus has been incorporated into the conditioned response (Janik and Slater, 2000). 'Pant hoot' calls made by chimpanzees frequently evolve as they incorporate vocal signals traditionally used in other situations (Marshall *et al.*, 1999). As they develop and mature, vervet monkeys learn the context of which alarm calls correspond to specific predators (Seyfarth and Cheney, 1986). Changes can also be temporal, such as stereotyped series of clicks produced by sperm whales (*Physeter microcephalus*) known as 'codas' (Watkins and Schevill, 1977). These clicks are arranged into new patterns or rhythms depending upon the

context in which they are produced. Production learning involves using a modified or completely novel signal following exposure to signals made by conspecifics (Janik and Slater, 2000). This can be seen in species that progressively change their vocal patterns. The songs of humpback whales constantly evolve as individuals conform to the ever-shifting signals produced by others (Payne and Payne, 1985). Infant horseshoe bats (*Rhinolophus ferrumequinum*) use echolocation calls at the same frequency as their mother, believed to assist in mother-offspring recognition (Jones and Ransome, 1993). In both cases, individuals evolve their respective vocal patterns through modification or innovation. However, a lack of controlled or conditional experiments makes vocal categorizations hard to differentiate.

The vast majority of work done on vocal learning and culture involves songbirds (Slater, 1986), though other examples include mammalian species such as bats (Jones and Ransome, 1993), chimpanzees (Marshall *et al.*, 1999), and killer whales (Deecke *et al.*, 2000). Dialects are defined as variations to a specific vocal display which differ based on defined boundaries of separation (Rothstein and Fleischer, 1987). Often these boundaries are geographic, but they can also be social or genetic. Acoustic clans in killer whales produce separate dialects based on matrilineal relation. Although they come from the same geographic locations and interact with one another for mating, the genetic barrier keeps their dialects distinct (Deecke *et al.*, 2000). These barriers are not impenetrable; an individual can leave their population and join another. Often what happens in those cases is that the immigrant individual will learn and adopt the local dialect (Payne, 1985). This implies that, although dialects are relatively unchanging, it is not because the individual is incapable of changing it.

Several factors play a part in the development and maintenance of dialects for songbirds. Learning dialects usually takes place in males during a critical or sensitive period within the first year or two of life (Nottebohm, 1970; Beecher and Brenowitz, 2005). Young males require auditory feedback to help the learning process. In subsequent years the song patterns become fixed (Nottebohm, 1970). These songs are often involved in sexual selection. In cases of intra-sexual selection, males direct the song at other males as a means of competing or establishing territory. Songs are also used in intersexual selection to attract females (Catchpole and Slater, 2008). Some dialects may assist breeding by providing a method of distinguishing which individuals belong to the local population, thus promoting genetic diversity (Nottebohm, 1970). Environmental variability could also influence how the song is structured, particularly since barriers are

instrumental in the development of dialects and these barriers are commonly geographic (Kroodsma, 2004).

1.4 Complexity in vocal learning

The repertoire, arrangement, and structure of vocal displays vary greatly among species. Some have simple arrangements that contain only a few elements. Others have many elements that may be arranged in a number of ways. The variety within a display is often described as its 'complexity'. However, complexity can be difficult to quantify as there is no singular definition (Kershenbaum, 2014). Repertoire is the simplest and most prevalent metric for assessing complexity (Nowicki *et al.*, 1998), defined by variables such as the total number of elements, the number of unique elements, and display duration (Boogert *et al.*, 2008; Cholewiak *et al.*, 2013; Templeton *et al.*, 2014; Murray, 2015). Another approach is to use information theory, which measures predictability in sequences of events (Shannon, 1948). Although Shannon (zero-order) entropy is not a reliable metric, higher-order estimates can quantify complexity in sequential arrangements of vocal signals (Shannon, 1948; Briefer *et al.*, 2010; Kershenbaum, 2014; Kershenbaum *et al.*, 2014a). The Lempel-Ziv metric quantifies the diversity of sequential patterns present, but is limited by sample size (Lempel and Ziv, 1976). Markov entropy rate measures diversity in the transitions between signals (Kershenbaum, 2014). The appropriate measure or combination of measures is dependent upon a number of factors such as repertoire size, sequential structure, sample size, or the behavioural process being investigated.

Many ecological factors influence the degree of complexity present in a vocal display. The 'social complexity hypothesis' suggests that a more complex display indicates a more complex social structure (Freeberg *et al.*, 2012). For example, a review of alarm calls in a number of sciurid rodent species (ground squirrels [*Spermophilus* spp.], prairie dogs [*Cynomys* spp.], and marmots [*Marmota* spp.]) found that call repertoire size positively correlated with social complexity index (Pollard and Blumstein, 2012). Information content can also influence complexity, as the intended message of the display may change with context. Wild chimpanzees have a repertoire of call combinations which are used in specific situations to convey different messages (Crockford and Boesch, 2005).

In many song displays, which are typically driven by sexual selection, complexity indicates the quality of the singer through positive correlation with male fitness (reviewed in Searcy, 1992). Metrics for fitness can be morphological (e.g. wingspan , weight, or body condition (Lampe and

Espmark, 2003; Kipper *et al.*, 2006; Pfaff *et al.*, 2007)), behavioural (e.g. parental effort or offspring survival (Hasselquist *et al.*, 1996)), or neurological (e.g. stress response (DeVoogd, 2004) or learning capacity (Boogert *et al.*, 2008)). Correlation with such a variety of fitness indicators allows females to use complexity during sexual selection to decide between competing males (Nowicki *et al.*, 1998; Woodgate *et al.*, 2012; Suzuki *et al.*, 2014). Preference for more complex songs often drives males to increase their song complexity to stand out among their competitors (Searcy, 1992; Catchpole, 1996; Mountjoy and Lemon, 1996; Spencer *et al.*, 2005).

1.5 Syntactic rules in vocal communication

The complexity of a display is often influenced by its syntactic or grammatical rules which govern how signals are arranged. These rules are grouped into four classes known as the Chomsky hierarchy of formal grammars (Chomsky, 1957). At the bottom of this hierarchy are the simplest rules, known as 'regular' grammar. They are characterized by movement between a finite number of signals or sequences (Kershenbaum *et al.*, 2014a). Movements fall into two categories: deterministic or probabilistic (Kershenbaum *et al.*, 2014b). Deterministic movements occur when a sequence is fixed and known, meaning that signal B will always follow signal A. Probabilistic movements are sequences that have a certain probability of occurring. For example, the letter Q is not always followed by the letter U in English, but there is a certain probability that "QU" will occur. Regular grammars occur in most animal communication systems and vocal displays (Kershenbaum *et al.*, 2014a). The second class of formal grammar is known as 'context-free' grammar (Chomsky, 1957). These rules are more complex because signals in a sequence can impact one another, and therefore they require information retention (Chomsky, 1957; Kershenbaum *et al.*, 2014a). For example, if two signals must repeat the same number of times (e.g., AAABBB), the individual must remember how many times 'A' repeats in order to know how many times 'B' must repeat. Such rules allow for nested or 'recursive' patterns: one meaningful sequence may be embedded within one another or signals may combine in multiple ways (e.g., the way words are embedded or combined within sentences) (Briefer *et al.*, 2010; Kershenbaum *et al.*, 2014a). Context-free grammar is thought to be restricted to human language. 'Context-sensitive' grammar, the third grammar class, is merely a more complex extension of context-free grammar in which recursive patterns get longer and more complicated (Chomsky, 1957; Briefer *et al.*, 2010). All human languages are encompassed by context-sensitive grammars (Briefer *et al.*, 2010). Finally, 'recursively enumerable' grammar is the most complex set of rules and only occurs in the context of machine learning (Chomsky, 1957; Briefer *et al.*, 2010). 'Regular' and 'context-free' grammars are the two hierarchies most relevant to animal communication and language evolution.

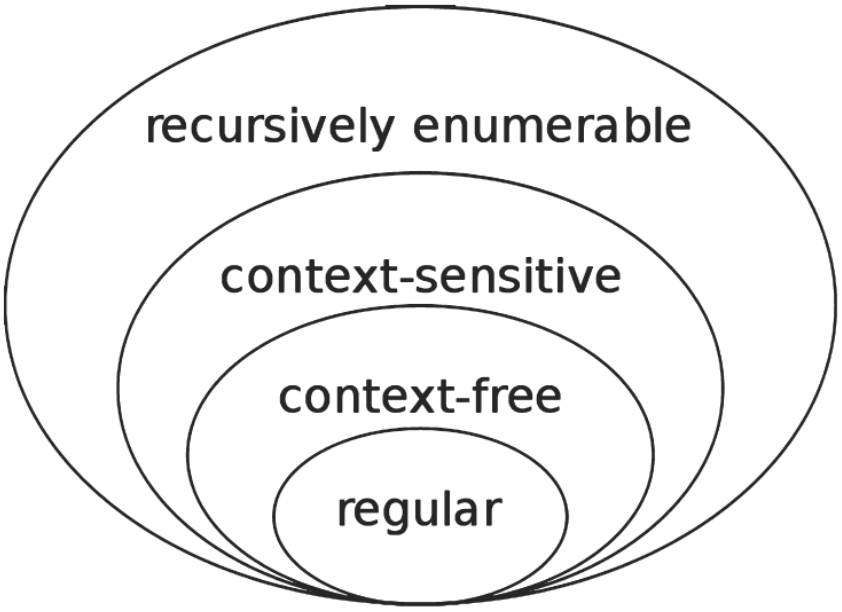

Figure 1.1: The Chomsky hierarchy of grammar classes (Chomsky, 1957)

Basic syntax has been shown in bird species such as black-capped chickadees (*Parus atrzcapzllus*) (Hailman and Ficken, 1986), but the bulk of studies on syntactic structure in animals have focused on song displays in birds (Catchpole and Slater, 2003). These songs are complex, often with large repertoires and variation in their structure. It is believed that, as with most animal communication, syntax in birdsong follows regular grammar. Gentner *et al.* (2006) challenged this assertion by claiming to show 'context-free' grammar in European starlings (*Sturnus vulgaris*), but that claim has been subsequently debated (van Heijningen *et al.*, 2009). Only a few studies have analysed syntax in mammalian species. Studies focus on primates (e.g., titi monkeys [*Callicebus moloch*] (Robinson, 1979), vervet monkeys [*Cercopithecus aethiops*] (Seyfarth *et al.*, 1980), wedge-capped capuchin monkeys [*Cebus olivaceus*] (Robinson, 1984), wild gibbons [*Hylobatidae* spp.] (Clarke *et al.*, 2006)) and cetaceans (e.g., killer whales, Shapiro *et al*., 2011; bottlenose dolphins [*Tursiops truncatus*], Janik, 2009) due to their perceived cognitive abilities. The two other mammals shown to have syntax are free-tailed bats (*Tadarida brasiliensis*) (Bohn *et al.*, 2009) and rock hyrax (*Procavia capensis*) (Kershenbaum *et al.*, 2012). While most mammals display regular grammar, there is some limited evidence to suggest the presence of context-free grammar in captive species such as bottlenose dolphins (Herman *et al.*, 1984) and bonobos (*Pan paniscus*) (Savage-Rumbaugh *et al.*, 1993). However, context-free grammar in non-human mammals has yet to be widely accepted. A broader range of mammalian species in syntactic studies will provide comparative information on the development of syntax across species and enhance the understanding of its development in humans.

1.6 Network structure

Recent studies employing syntactic analyses have begun to include components such as network structure. Networks are a collection of points or 'vertices' that are connected by a relationship (Newman, 2003). These networks can be comprised of almost anything: neural pathways, genetic relatedness, or social relationships. For example, a social network could be made up of people (the vertices) that are connected by how much time they spend together. While two people may not know each other, they might be connected by a number of "steps" or mutual acquaintances. In the context of a vocal display, the "vertices" are the vocal signals and the connections are the transitions between them (e.g., in the sequence 'ABC', A connects to B, B connects to C, and A is connected to C by one step). Some networks are randomized, meaning there is no order to how vertices are connected (Rapoport, 1957). At the opposite end of the scale, networks can be 'regular' where all vertices are equally connected (Watts and Strogatz, 1998; Newman, 2003). Random networks are characterized by poor clustering with few steps between any of the vertices, while regular networks have high clustering among certain vertices but often require many steps to connect vertices in separate clusters (Newman, 2003). The nature of these connective relationships can be quantified using network modelling techniques. Network features include clustering (i.e., how frequently groups of vertices are connected), path length (i.e., how many steps connect any two vertices), and transition directions (i.e., whether one signal tends to precede or follow another) (Sasahara *et al.*, 2012).

Between the extremes of completely random or completely regular networks lie "small-world" networks, which contains characteristics of both (Watts and Strogatz, 1998). Small-world networks have a high amount of clustering between certain vertices (similar to regular networks), but a short number of steps between any of the vertices (similar to random networks) (Watts and Strogatz, 1998). A popular illustration of small-world structure is known as 'six degrees of separation". The idea behind this is that any two individuals in the world are connected by six or fewer acquaintances (Guare, 1990; Watts and Strogatz, 1998). Milgram (1967) demonstrated this by asking participants to pass a letter to a specific target individual through first-name acquaintances. Supporting the concept of "six degrees of separation", letters reached their targets by passing through an average of six people.

Small-world networks are ubiquitous among a wide array of complex systems. These systems can be biological, such as the functional network of cortical hubs in the human brain (Achard *et al.*, 2006). They also occur in information systems such as human language (Cancho and Solé, 2001) or

email communications (Adamic and Adar, 2005). Even artificial constructs such as urban street planning (Jiang and Claramunt, 2004) result in small-world arrangement. Recent work has found that small-world networks are common in several bird species with songs containing complex repertoires (Sasahara *et al.*, 2012; Weiss *et al.*, 2014; Taylor and Cody, 2015; Cody *et al.*, 2016). Its prevalence suggests that small-world networks may be present in other complex vocal displays. Studies are needed which explore network structure outside of oscine species. Small-world structure is thought to indicate a possible structural convergence among complex song displays (Bolhuis *et al.*, 2010; Hedley, 2016) and may provide insight into the processes behind them (Deslandes *et al.*, 2014; Weiss *et al.*, 2014; Cody *et al.*, 2016), though studies have only just begun to clarify what those insights might be.

1.7 Study species: humpback whales

Whales, dolphins, and porpoises all belong to the order Cetacea and fall into two main groups: odontocetes (toothed whales) and mysticetes (baleen whales) (see review in Berta *et al.*, 2005). Humpback whales are mysticetes which reach lengths of 15m and weigh approximately 25-30 tonnes (Winn and Reichley, 1985). The baleen plates in their mouths filter water, allowing them to feed on krill or small schooling fish such as herring or mackerel. Feeding takes places at high latitude feeding grounds during the summer months (Dawbin, 1956; Johnson and Wolman, 1984; Winn and Reichley, 1985). As winter approaches, they undertake one of the longest known migrations of any mammal and head to low latitude breeding grounds to mate and give birth (Dawbin, 1956; Tyack and Whitehead, 1983; Payne and Payne, 1985; Clapham, 1996). While on the breeding grounds, individuals fast due to a lack of available prey at these lower latitudes (Clapham, 1996). Sexual maturity occurs at approximately 5 years of age, although females may first give birth somewhere between 5 and 10 years old (Johnson and Wolman, 1984; Clapham, 1996; Gabriele *et al.*, 2007). Between fasting and an 11 month gestation period, reproduction can be taxing on females and thus birth intervals are usually 2-3 years (Clapham and Mayo, 1990). However, annual births have been reported in Hawaii (Glockner-Ferrari and Ferrari, 1990; Straley *et al.*, 1994). Humpback whales are thought to have a 'floating lek' mating system (Herman and Tavolga, 1980; Clapham, 1996; Herman, 2017) because although males compete with each other for females through displays (Tyack and Whitehead, 1983; Herman *et al.*, 2007) as seen in typical lekking systems (Höglund and Alatalo, 1995), they lack the requisite spatial territories (Helweg and Herman, 1994; Craig and Herman, 2000). Floating leks show elements of both polygynous (one male, multiple females) and promiscuous (multiple males and females) mating strategies without completely conforming to either (Clapham and Palsbøll, 1997; Cerchio *et al.*, 2005).

The populations of the Southern Hemisphere utilize six different feeding grounds (Areas I-VI) throughout the Antarctic. These groupings further divide into breeding stocks (Groups A-G) based on the breeding grounds they frequent (IWC 2005). Migrations between these areas follow a corridor that runs along the coasts of New Zealand, heading north during June and July and south in September and October (Dawbin, 1956; Paterson and Paterson, 1984). Maternally directed site fidelity to both breeding and feeding grounds have been identified in North Pacific humpback whales, making them reliable indicators for distinct populations or sub-groups (Calambokidis *et al.*, 2001). This thesis will focus on two stocks from the Area V feeding ground (Figure 1.2). Group E1 has an estimated 25,000 individuals (Noad *et al.*, 2016) and winters in breeding areas off the eastern coast of Australia (Bannister *et al.*, 2008). Group E2 winters off of the Pacific island of New Caledonia (IWC 2005) and is a much smaller group, comprised of approximately 500-800 individuals (Garrigue *et al.*, 2001). Despite the overlap in both feeding area and migratory paths, there is low interchange between the east Australia and New Caledonia populations (Garrigue *et al.*, 2011b). Furthermore, DNA analyses have shown these populations to be genetically distinct (Olavarría *et al.*, 2007).

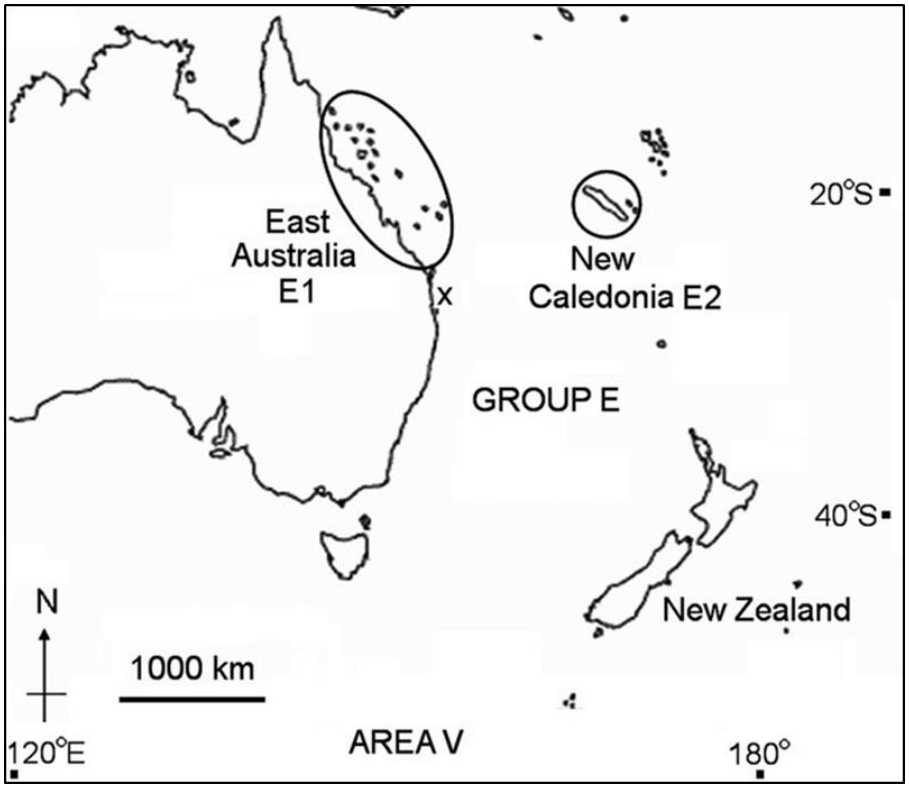

Figure 1.2: Map showing the study populations belonging to Group E, as identified by the International Whaling Commission. East Australia (E1) and New Caledonia (E2) indicate the breeding grounds for each respective population, both of which feed in the Area V feeding ground of Antarctica. Map presented here is modified from Garland *et al.* (2015)

Humpback whales are an excellent model for social transmission in animals due to several factors. Their songs are particularly complex, making their learning process more developed than those in other mammalian species. Most species socially transmit behaviours over a short distance, often due to constraints on the visual or acoustic contact required for transmission. Humpback whales on the other hand learn their songs across a rather exceptional spatial scale of hundreds of kilometres with strong directionality (Rendell and Whitehead, 2001; Garland *et al.*, 2011). This occurs with unprecedented speed and consistency, indicating the strength of the learning mechanism. In addition to their song, humpback whales have demonstrated several additional cultural traits. A foraging strategy in a North Atlantic population spreads through social transmission (Allen *et al.*, 2013), while site fidelity is maternally directed (Baker, 1986; Clapham, 1996; Calambokidis *et al.*, 2001; Garrigue *et al.*, 2011a; Rosenbaum *et al.*, 2017). This indicates that culture plays a key role in multiple aspects of humpback whale ecology, making them an ideal example for the study of its influence on behaviours in non-human species.

1.8 Humpback whale song

Humpback whale songs are sung exclusively by males and primarily occur in the breeding grounds, though they can be heard in feeding areas (Mattila *et al.*, 1987; Clark and Clapham, 2004; Stimpert *et al.*, 2012; Vu *et al.*, 2012; Garland *et al.*, 2013a) and along migration routes (Payne and McVay, 1971; Mattila *et al.*, 1987; Noad, 2002; Smith, 2009; Garland *et al.*, 2011). Songs have a nested hierarchical structure (Payne and McVay, 1971). Individual sound 'units' are the smallest measure, although some further divide these into 'subunits'. These units have a broad range of acoustic features that vary greatly between unit types. Fundamental frequencies range from 30 Hz to approximately 5 kHz (Hafner *et al.*, 1979; Payne and Payne, 1985; Mednis, 1991), with harmonics reaching 24 kHz (Au *et al.*, 2006). Durations are typically between 0.1 and 4.2 seconds (Cato, 1991; Adam *et al.*, 2013), and source levels (rms) are from 150 to 180 dB re 1µPa2 @1m (Au *et al.*, 2006; Risch *et al.*, 2012; Girola *et al.*, In Review) depending, to some extent, on the frequency of the unit (Girola *et al.*, In Review). Units repeat in a predictable set of patterns that make up a 'phrase'. Phrases then repeat several times to form a 'theme'. A stereotyped set of 5-9 themes sung in a particular order without repetition make up a 'song cycle' (Payne and McVay, 1971; Payne and Payne, 1985; Cholewiak *et al.*, 2013). A song cycle can last between 7 and 30 minutes, continuously repeating in a 'song session' that can last for hours (Payne and McVay, 1971). Certain aspects of the song are more stable than others. Units tend to vary in their acoustic features such as length, duration, frequency, and harmonic complexity. Themes can be placed into one of three separate categories (Payne and Payne, 1985). A theme that remains consistent in its

phrase repetitions is a ‘static theme’. If a theme gradually changes with each successive phrase repetition, it is known as a ‘shifting theme’. Occasionally themes will have no consistency to them, known as ‘unpatterned themes’. The number of times a phrase is repeated within a theme varies and is thought to be context-dependent (Smith, 2009). The order in which themes occur remains consistent, although individuals may occasionally skip or omit a theme during a particular song cycle (Payne and Payne, 1985). Partial or complete similarity in songs corresponds to meta-population structures (Cerchio *et al.*, 2001; Garland *et al.*, 2013b; Darling *et al.*, 2014). Populations without apparent exchange or acoustic contact share no song similarity. Thus, the songs sung in the Hawaiian Islands differ from those sung in the Caribbean, which differ from those sung in the South Pacific (Cholewiak *et al.*, 2013).

Despite considerable study, song function is currently unknown. Speculations focus on inter-sexual selection like that seen in bird songs, in which females use song display to assess male fitness or quality (Payne and McVay, 1971; Tyack, 1981; Payne *et al.*, 1983; Smith *et al.*, 2008). For example, singers in east Australia tended to join mother-calf pairs more than other conspecifics and primarily stopped singing when joined by other males (Smith *et al.*, 2008). Intra-sexual communication between males has not been discounted, such as dominance displays (Darling and Bérubé, 2001), male cooperation (Darling *et al.*, 2006; Dunlop and Noad, 2016), or spacing between males (Winn and Winn, 1978). Several studies have reported singing males being approached by other males (Tyack and Whitehead, 1983; Darling and Bérubé, 2001; Darling *et al.*, 2006), while few studies have found similar results with females (Medrano *et al.*, 1994). A multi-message signal, similar to that seen in birdsong (Catchpole and Slater, 2008), has been proposed which suggests that the song has multiple meanings and therefore potentially multiple functions (Murray, 2015; Herman, 2017). However, the specific information content of the song remains unclear, as well as how that information might be perceived by receivers (whether they are male or female) (Tyack, 1981).

An unusual feature of the humpback whale song is that it has both conformity (i.e. stability in a behaviour among individuals) and plasticity (i.e. changes or flexibility in a behaviour). All the individual males within a given population sing the same song arrangement (Payne and Payne, 1985). The song itself changes progressively (Payne and Payne, 1985), with changes occurring at any level of the song. Units may be stretched, contracted, multiplied, or omitted (Payne *et al.*, 1983; Payne and Payne, 1985; Guinee and Payne, 1988). Phrases or themes can be modified, repeated, added in or dropped (Winn and Winn, 1978). The village indigobird (*Vidua chalybeata*)

and the Panamanian yellow-rumped cacique (*Cacicus cela*) (Trainer, 1989) are the only two documented species with a similar dichotomy in the evolution of their songs within a colony.

Novelty and stability appear to be the drivers behind song changes. For many populations, stability tends to culminate in the songs of adjacent years (Payne and Payne, 1985). The South Pacific populations have 'cultural revolution events' in which the entire population makes a sudden and radical change to the song and replace it with a newly introduced one (Noad *et al.*, 2000). This demonstrates the malleability of songs and how quickly shifts can occur. Partial similarity in songs from different populations suggests that some parts of a song may be more susceptible to changes than others, but what dictates this varying sensitivity is unknown (Darling *et al.*, 2014). Recent work suggests that songs may be learned using themes as 'building blocks', with changes occurring more often in unit sequences (Garland *et al.*, 2017a).

There is no answer to why one change is chosen and another is not, or why revolution events do not occur every year (Garland *et al.*, 2011; Rekdahl, 2012b). Studies in human psychology theorize that for any innovation to integrate into a cultural trend, it must have "optimal mismatch". This is the balance between similarity to the current norm and attractive originality (Payne, 2000; Whitehead and Rendell, 2014). The 'novelty-threshold hypothesis' suggests that a certain number of individual singers must adopt a change for it to be incorporated into the population's song (Noad, 2002). It is reasonable to speculate that changes benefit the singer in some capacity, with those benefits outweighing the costs of making changes. For example, making changes to the song pattern may help the singer stand out to potential mates (Krebs, 1977). Otherwise, there would be no motivation for continual alteration. Learning more about these changes could illuminate the potential benefits of a constantly changing display, as well as how the changes influence or modify the information content of the display. This could also give further insight into the role of the song in humpback whale ecology (Kaufman *et al.*, 2012).

There are two types of conformity: informational and normative (Deutsch and Gerard, 1955; Claidière and Whiten, 2012). Informational conformity occurs when an individual conforms to gain accurate information about reality in a non-social context. Normative conformity is driven by social interactions and adhering to social constructs. The distinction between the two has been explored extensively in human sociology and recently has become more integrated into studies of non-human species (Claidière and Whiten, 2012). Humpback whales have normative conformity within their songs, as demonstrated by the social mechanism of transmission (Noad *et al.*, 2000;

Garland *et al.*, 2011). However, conformity exists on a gradient and both forms of conformity may play a role. As with the plasticity of the songs, lack of knowledge regarding function presents the possibility that pieces of the song transmit non-social information alongside the social context it already has.

Humpback whale songs are a prime example of horizontal cultural evolution among non-human species (Noad *et al.*, 2000; Garland *et al.*, 2011; Whitehead and Rendell, 2014). Individuals learn the progressive changes from each other and spread them to others within the population (Payne *et al.*, 1983). This is also how the song passes from one population to another, indicating that cultural transmission reaches far beyond those that directly associate with one another (Garland *et al.*, 2011). Cultural revolutions further demonstrate the extent of plasticity in songs; the rapid change that occurred in 1996/1997 revolution event in the east Australian population seemed to be the work of just a few individuals from the west Australian population (Noad *et al.*, 2000). Additional revolution events originating from west Australia occurred in east Australia during 1999/2001, 2002/2003, 2005/2006, 2006/2007, 2008/2009, and 2010/2011(Garland *et al.*, 2011; Rekdahl, 2012b).

1.9 Inter-population exchange of humpback whale song

The South Pacific meta-population demonstrates a large-scale horizontal cultural transmission of song (Garland *et al.*, 2011). Transmission occurs in a unilateral direction from west to east across the populations, moving from east Australia to New Caledonia, Tonga, and American Samoa, then to the Cook Islands, and French Polynesia (Garland *et al.*, 2011). This directionality takes place independent of a song's stability or the presence of a revolution event. The mechanism for this transmission is not fully understood, as there is very little exchange of individuals between populations (Garrigue *et al.*, 2011b; Garland *et al.*, 2015). Suggested points of contact for song exchange include the shared Antarctic feeding grounds (Garland *et al.*, 2013a) or possibly along the migratory route (Constantine *et al.*, 2007; Garland *et al.*, 2013b). Not all meta-populations seem to exchange songs in this fashion. Populations in the North Pacific, specifically Hawaii and Mexico, have demonstrated synchronicity in the evolution of their songs, despite their geographic separation by several thousand kilometres (Cerchio *et al.*, 2001). Movement of song across multiple populations has not been documented in any other location worldwide (Garland *et al.*, 2011; Garland *et al.*, 2013b). Furthermore, the only other cultural transmission that occurs on such a large spatial scale is found in humans (Garland *et al.*, 2011).

There is a consistent one year delay in the transmission of songs between the neighbouring east Australian (E1) and New Caledonian (E2) populations (Garland *et al.*, 2011). The song pattern learned by the New Caledonia population does not appreciably change during this exchange (Garland *et al.*, 2011). Similar transmission also occurs from west Australia to east Australia with the same directionality and time delay, but has only been documented during revolution years (Rekdahl, 2012a). The broad scale transmission between east Australia and New Caledonia has been well studied (Garland *et al.*, 2011). Theme sequences remain intact as the song moves from one population to another, and this transmission is consistent for a large timescale. However, there is very little information about what happens during transmission on a fine scale (e.g., within unit sequences that comprise themes). East Australia is a migratory route with a very large population (~25,000) (Paterson and Paterson, 1984; Noad *et al.*, 2006), while New Caledonia is a breeding ground with a small resident population (~500) (Garrigue *et al.*, 2001). It is possible that differences may result in fine-scale variations, distinguishing each population's version of the same song. The presence or absence of such variation may provide insight into cultural transmission between populations.

1.10 Thesis outline

Chapter 2 is a methodology chapter which develops a classification technique to be used in all of the subsequent data chapters. An acoustic dictionary of prototype units is created using self-organizing map (SOM) classification. This dictionary represents the song repertoire for the study population over 13 consecutive years. Cartesian distances are measured between all unit types based on the SOM spatial layout to quantify similarity between those units. This methodology is then applied to new, unmeasured recordings, allowing for rapid transcription of data into numeric strings. By creating a robust and repeatable way to transcribe high volumes of data, sample size can be increased and classification can be standardized across chapters. Furthermore, this method can be applied to vocal repertoires across multiple species, addressing the use of acoustic dictionaries and quantified acoustic similarity in the broader study of vocal repertoires as well as in humpback whales. This chapter has been published in *the Journal for the Acoustical Society of America* (JASA).

Chapter 3 examines the patterns of repertoire complexity and second-order entropy within songs over time, transcribed using the methods outlined in Chapter 2. Prior to this thesis, trends in complexity had not been quantified in humpback whale songs. Songs become more complex as they progressively evolve over time, but become simpler when revolution events completely replace

the song. Entropy remains relatively consistent over time, indicating that predictability in song arrangement does not correlate with the level of complexity within the song. Complexity in song displays show fluctuation in a consistent pattern that corresponds to revolution events, indicating constraints on song learning ability.

Chapter 4 expands on the findings of Chapter 3 by looking at complexity in terms of syntax. Network structure, structural complexity, and syntactic arrangements are quantified in songs over the same 13 year period as Chapter 2 and Chapter 3. In every year, song arrangements display "small-world" network structure, often found in complex birdsongs and human language. These types of network structures remain consistently present over time, unlike the fluctuating song complexity results from Chapter 3. Structures may aid in the song learning process by supporting a combination of stability and diversity. Fine-scale network structure has not yet been examined in humpback whale song, and provides a comparison to the communication structures of other taxa.

Chapter 5 applies the analyses from Chapters 3 and 4 to two years of song from New Caledonia. Since song patterns move eastward in the South Pacific, the New Caledonian songs provide a comparison for the analogous songs in east Australia. This chapter shows high fidelity in song learning across multiple populations, with songs maintaining their degree of both song complexity (Chapter 3) and small-world structure (Chapter 4). The scale of the horizontal cultural transmission seen between these two populations provides a unique opportunity to examine the complexities of the same song arrangement when sung by separate populations. This is the first fine-scale comparison of inter-population song exchange, providing insight into the currently unknown mechanism of precisely where and how this song exchange occurs.

Chapter 6 is a general discussion which gives an overall summary of the results found in the previous four data chapters. Several avenues of future research that stem from the conclusions of this thesis are suggested. The significance of these results are detailed in the context of social learning and the body of work on animal cultural transmission.

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CHAPTER 2 Using self-organizing maps to classify humpback whale song units and quantify their similarity

2.1. Abstract

Classification of vocal signals can be undertaken using a wide variety of qualitative and quantitative techniques. Using east Australian humpback whale song from 2002-2014, a subset of vocal signals was acoustically measured and then classified using a Self-Organizing Map (SOM). The SOM created 1) an acoustic dictionary of units representing the song's repertoire, and 2) Cartesian distance measurements among all unit types (SOM nodes). Utilizing the SOM dictionary as a guide, additional song recordings from east Australia were rapidly (manually) transcribed. To assess the similarity in song sequences, the Cartesian distance output from the SOM was applied in Levenshtein distance similarity analyses as a weighting factor to better incorporate unit similarity in the calculation (previously a qualitative process). SOMs provide a more robust and repeatable means of categorizing acoustic signals along with a clear quantitative measurement of sound type similarity based on acoustic features. This method can be utilized for a wide variety of acoustic databases especially those containing very large datasets, and be applied across the vocalization research community to help address concerns surrounding inconsistency in manual classification.

2.2. Introduction

Acoustic signals are commonly used for communication in a variety of species and signals typically convey different kinds of information. Information can range from simple species identification (Gerhardt, 2001) to complicated ideas such as foraging (Slocombe and Zuberbühler, 2006) or social hierarchy (Catchpole and Slater, 2008). Vocal studies are therefore imperative to understanding a broad range of concepts such as species distribution, signal information content, or vocal learning. One major hurdle for any vocalization study is a precise means to analyze data (Kershenbaum *et al.*, 2014a). Acoustic features such as duration or frequency can be quantified (Tchernichovski *et al.*, 2000; Cerchio *et al.*, 2001),yet these features do not always provide complete signal representation (Janik, 1999). As a result signals are often classified into categories qualitatively by a human observer (Janik, 1999; Kershenbaum *et al.*, 2014a).

Manual classifications can be corroborated by several means. Naïve matching tests compare agreement between independent observers (e.g., Garland *et al.*, 2011). Quantitative testing can also assess manual classification, including multivariate statistics such as discriminant function analysis (DFA) (e.g., Dunlop *et al.*, 2007), Classification And Regression Trees (CART) (e.g., Melendez *et al.*, 2006, Rekdahl *et al.*, 2013) or Random Forest analysis (e.g., Risch *et al.*, 2013, Garland *et al.*, 2015). Despite quantitative support, classifying signals remains largely qualitative. Automated methods provide more objectivity, but cannot always be implemented if signals are too varied or complex (Janik, 1999). Subjectivity is a key weakness in vocalization studies: it impedes standardized classification across studies of the same vocal display, and there is no reliable way to determine if classifications are biologically relevant to the study species. Different methods are therefore required that can move classification towards a more repeatable and objective approach.

One such technique is an artificial neural network called a Self-Organizing Map (SOM) (Kohonen, 1990). What makes the SOM such a beneficial tool is that it uses an "unsupervised" learning algorithm: there is no parameter selection of the data's variables or user feedback involved in the target classification outputs (Suzuki *et al.*, 2006; Green *et al.*, 2007; Kohonen, 2014). Unsupervised learning removes a degree of the subjectivity that can come from predetermining how to group information, which occurs in "supervised" learning (Kohonen, 1990; Green *et al.*, 2007). It also allows for the possibility of recognizing patterns that may not be apparent to a human observer (Green *et al.*, 2007). This is advantageous given the aforementioned difficulty with determining a feature's biological relevance.

SOMs organize information into a 2-dimensional "output space" (Bauer and Pawelzik, 1992), made up of 'nodes' which serve as the categories into which data will be grouped. Before this can happen, the map must learn to classify the dataset in question. Acoustic signals within the dataset are each represented by an input vector of values (i.e. each vector is the list of measured variables). Training occurs by repeatedly presenting the map with each of the input vectors. Each node contains a weight vector of the same length as the input vectors, and the nodes learn to respond to the data during training (Kohonen, 1990). A principal component analysis on the input vectors provides initial values for the weight vectors (Hagan *et al.*, 1996; Kohonen, 2014). SOMs can then place a signal into whichever node has the weight vector that best matches its input vector (Kohonen, 1990; Walker *et al.*, 1996). The spatial arrangement of the nodes is dictated by two parameters: neighborhood size and learning rate. Learning rate controls the extent to which a node is altered, while neighborhood size determines how many surrounding nodes are affected by those alterations (Hagan *et al.*, 1996; Callan *et al.*, 1999). The result is that more similar nodes are arranged to have closer proximity to one another within the map. An added advantage of this spatial arrangement is that the distance between nodes can be measured in either Euclidean or Cartesian space. These measures serve as a means of quantifying similarity between sound types, which can then be utilized in subsequent analyses (Garland *et al.*, 2017b). SOMs have been used as a method for analyzing vocal signals in species such as domestic pigs (*Sus scrofa)* (Schön *et al.*, 2001), white-crowned sparrows (*Zonotrichia leucophrys pugetensis*) (Ranjard and Ross, 2008), and humans (Callan *et al.*, 1999).

SOMs appear particularly useful in the classification of humpback whale song units (Walker *et al.*, 1996; Mercado and Kuh, 1998; Suzuki *et al.*, 2006; Green *et al.*, 2007; Kaufman *et al.*, 2012; Murray *et al.*, 2018). Humpback whale song has a hierarchical structure consisting of sound units repeating in a set pattern to make up a phrase. Phrases then repeat a number of times to form a theme. Themes are repeated sequentially to make up a song cycle (Payne and McVay, 1971; Payne and Payne, 1985; Cholewiak *et al.*, 2013). Although all males in a population typically sing the same song pattern at any given time, the song tends to change progressively (Payne *et al.*, 1983; Payne and Payne, 1985). Recent work by Murray *et al.* (2018) expanded on the use of acoustic features for song unit classification by measuring the frequency contours of tonal sounds, and including them as variables in the SOM classification. Classification results were then used to transcribe phrases into numeric strings to represent the unit sequences of those phrases. The Levenshtein distance, a similarity analysis that is highly suited to comparing vocal sequences

(Kershenbaum *et al.*, 2014a), was then used between transcribed sequences along with cluster analyses to quantitatively identify themes.

The degree of complexity and rapid evolutionary change found in humpback whale song make it an ideal model to test the robustness and repeatability of this methodology in highly complex vocal displays. While similar prototypes have been generated before (Walker *et al.*, 1996; Mercado and Kuh, 1998), the current study expands on this by creating an acoustic dictionary, a task that has yet to be undertaken in vocalization research (Placer *et al.*, 2006). The size of many acoustic datasets often makes it impractical to measure every signal required to generate large sample sizes of vocal sequences. A dictionary can serve as a guide for the rapid transcription of new, unmeasured recordings into numeric sequences, bolstering sample size. Additionally, by applying SOM distance measurements that provide a quantitative measure of unit similarity in higher-level (sequence) analyses, the utility and repeatability of transcription using this dictionary is apparent. The relative efficiency of SOM classification is also investigated in comparison to the manual classification method when based on the same input data. Use of the SOM method described here provides a more repeatable and robust means of classifying acoustic signals, along with the application of quantified signal similarity in higher-level analyses in the complex song hierarchy. The current study aims to 1) to create an acoustic dictionary of humpback song units for one population over multiple years, 2) extract a means of quantifying similarity between those song units, 3) test the classification of sounds by the SOM against qualitative classification using CART and RF analyses, and 4) use sequence analysis to demonstrate the utility of applying both the acoustic dictionary and quantitative similarity measures to new recordings.

2.3. Methods

2.3.1. Study sites

Data used in the current study were collected off the coast of Peregian Beach (26°30’ S, 153°05’ E), located on the Sunshine Coast in Queensland, Australia (Fig. 2.1a) as well as Point Lookout (27°43’ S, 153°53’ E), located on North Stradbroke Island, Queensland, Australia (Fig. 2.1b). Both locations are along the migratory corridor of east Australian humpback whales where the whales often swim within a few kilometers of the shoreline (Paterson and Paterson, 1984; Noad and Cato, 2001).

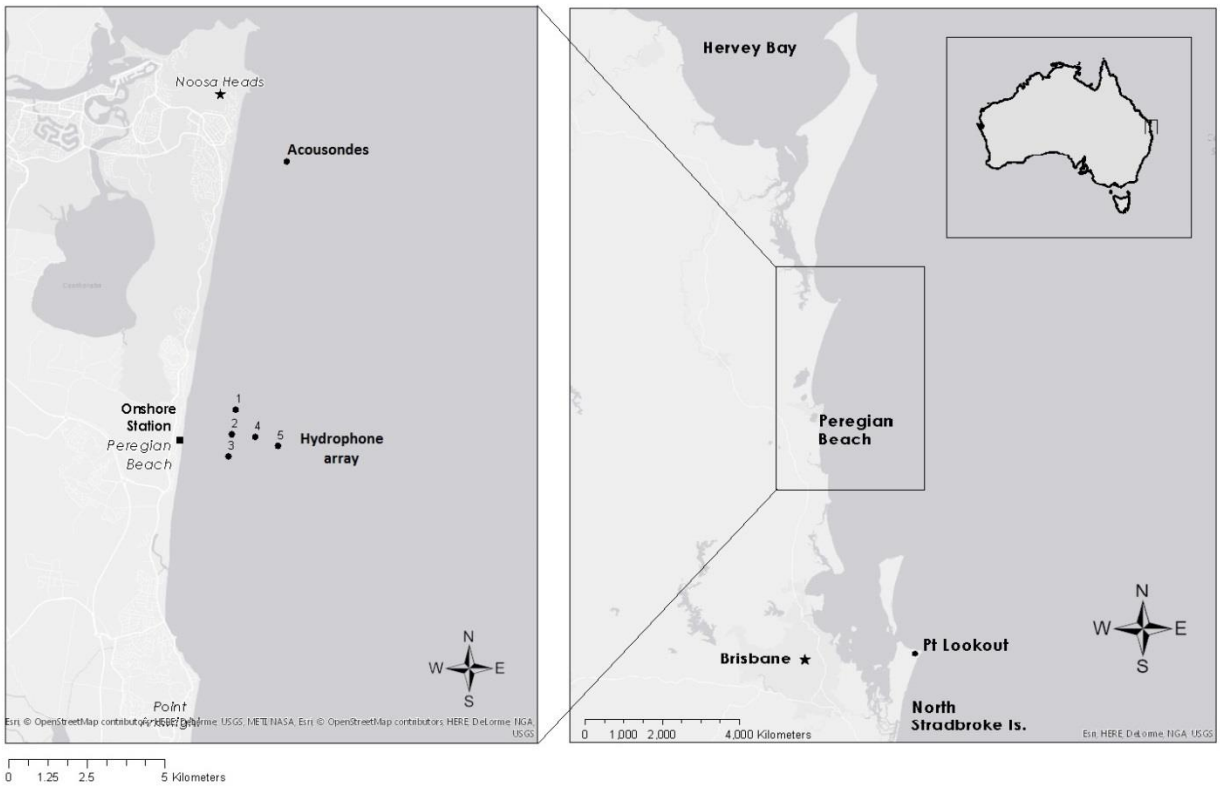


Figure 2.1 East Australia study sites: Peregian Beach and Point Lookout. The panel on the left shows the placement of the hydrophone array (hydrophone buoys are numbered 1-5) and the autonomous recorder deployments. The panel on the right shows the relative distance between the two study sites.

2.3.2. Data collection

Recordings from 2002-2014 were made using several platforms. A moored hydrophone array consisting of five buoys was deployed off of Peregian Beach in 2002-2004, 2008-2011, and 2014 (Fig. 2.1a). Each buoy had a High Tech HTI-96-MIN hydrophone with a built-in pre-amplifier (+40 dB), a customized amplifier (+20 dB), and a VHF radio transmitter (AN/SSQ-47A). They were set up 1.5 -2.5 km from shore, spaced approximately 750 m apart at depths of 18-28 m. Buoy signals were received at an onshore base station using a four-channel type 8101 Sonobuoy VHF receiver (buoys 1-4), or a single channel Sonobuoy frequency converter connected to a commercial FM radio receiver (buoy 5). Signals were digitized using a National Instruments E-series data acquisition card and recorded to a desktop computer with *Ishmael* acoustic software (Mellinger, 2001) at a sampling rate of 22 kHz, 16 bit depth, and stored as multi-channel WAV files. These recordings were supplemented with boat-based recordings using Cleavite CH17, GEC Marconi SH101X, or High Tech Inc. HTI-96-MIN hydrophones connected to Sony DAT, Microtrack, or Zoom digital recorders (generally using 44.1 kHz sampling rate, 16 bit depth, frequency response 30 Hz-20 kHz). Boat based recordings were the sole source of data in 2005-2007.

Autonomous underwater acoustic recorders were placed off the coast of Peregian Beach in 2012-2014. Each of the two recorders (Acousonde 3A with external battery housings, Greenridge Sciences, www.acousonde.com) had a sampling rate of 25,818 Hz with a 9 kHz low pass filter and a gain of 20 dB. All recordings covered the frequency range of humpback whale song. Both Acousondes were placed in the same location, approximately 1.5 km from the shoreline (Fig. 2.1a). Each was set on alternate 12 hour duty cycles, resulting in essentially continuous recording for the duration of each deployment.

2.3.3. Measurement of acoustic features of sound units

Recordings of songs were visualized as spectrograms in Raven Pro 1.4 (www.birds.cornell.edu/raven) using a Fast Fourier Transforms with Hann window, and 90% overlap. Good quality spectrograms were defined by a signal-to-noise ratio (SNR) of at least 10 dB above the background noise. Six complete song cycles from a singer in each year (2002-2014) were selected for measurement. Themes, phrases, and units were identified based on the accepted hierarchical structure of humpback whale song as described in Payne and McVay (1971). The exception was 2007, in which only four song cycles were selected due to a lack of available, high quality recordings. This resulted in 76 complete song cycles from 13 individuals being selected for acoustic measurement. From each of the six song cycles in a given year, three phrase repetitions of each theme were selected for measurement based on the highest quality repetitions within the recording (high SNR). The aim of the current study was to create a set of general representative sound types, and thus every atypical signal need not be represented. A subsample of phrase repetitions addresses variability found within themes while preventing overrepresentation of themes whose phrases are repeated with disproportionately high frequency. Further, the three phrase repetitions were taken from the beginning, middle, and the end of the theme to account for shifting themes that change subtly over multiple repetitions (Payne and Payne, 1985). A total of 3720 phrases from the 76 complete song cycles were selected and utilized for acoustic measurement.

Sound units were separated into two groups prior to measurement, contoured and non-contoured, which have distinctly different feature profiles (Dunlop *et al.*, 2007; Murray *et al.*, 2018). Separate methods were used in order to measure the acoustic features of each sound type in more detail (following Murray *et al.*, 2018). Contoured units have a definitive and traceable shape, such as tonal and harmonic units, as well as complex units containing both broadband and harmonic elements (see examples in Fig. 2.2a) (Dunlop *et al.*, 2007). Non-contoured units have no traceable shape or harmonic elements, such as purely broadband and pulsed calls (see examples in Fig. 2.2b).

The decision to separate units allows for the use of contour tracing software, which provides multiple frequency measurements along the contour of a sound. This results in a more comprehensive representation of tonal and complex sounds by quantifying a signal's shape. A frequency contour cannot be generated for non-contoured units due to the lack of a traceable shape, necessitating the use of two different methods of measurement.

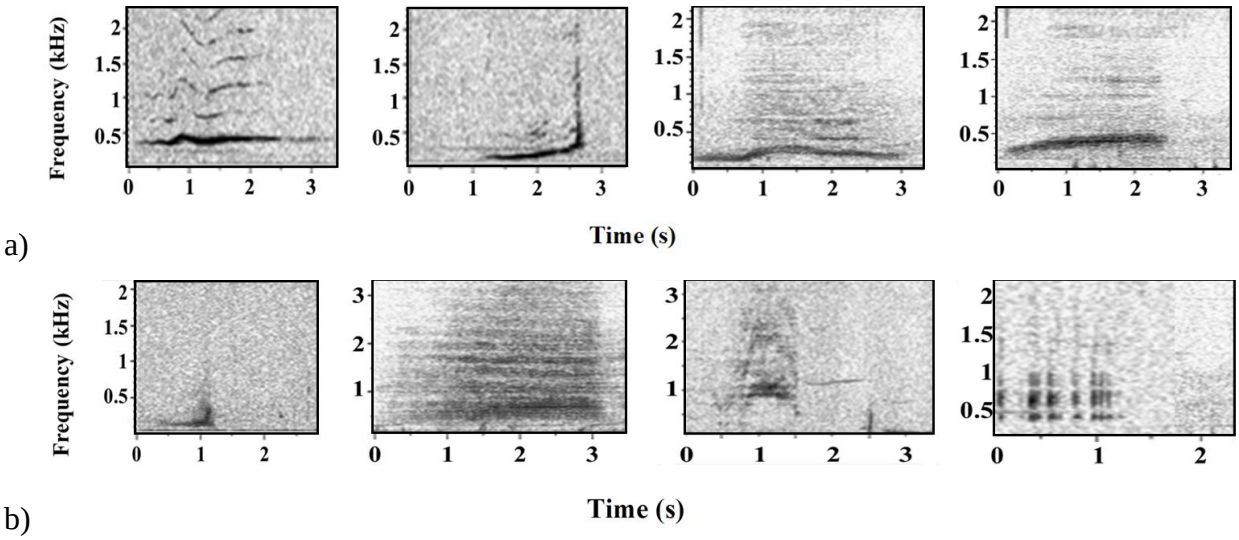
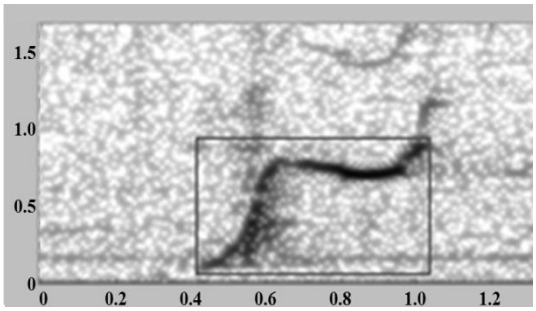


Figure 2.2 Spectrogram examples of a subset of the a) contoured and b) non-contoured units. All spectrograms were generated in Raven Pro 1.4 using 2048 FFT, Hann window, 90% overlap

2.1.Contoured feature measurement

Contoured sound units were measured using the frequency contour tracing program *Beluga* (http://biology.standrews.ac.uk/soundAnalysis/), within *MATLAB 2014b* (The MathWorks Inc, 2014). Recordings were imported into *Beluga* as WAV files. A spectrogram was calculated using an FFT of 2048, frame length of 1024, 93.75% overlap between frames, and Hanning window function. A tracing box was placed around the entire signal (Fig. 2.3a), and the recording was filtered to remove the average noise spectrum. The frequency contour was extracted using the "peaks" method without harmonics, measuring peak frequency every 0.03 seconds along the signal and creating a vector with a length analogous to the unit's duration (Fig. 2.3b). SOMs require vectors of equal length; therefore, contour vectors were truncated by extracting fifty equally spaced points along the vector. Each point was treated as a separate variable, similar to the computations method of classification developed by McCowan (1995).

a) 

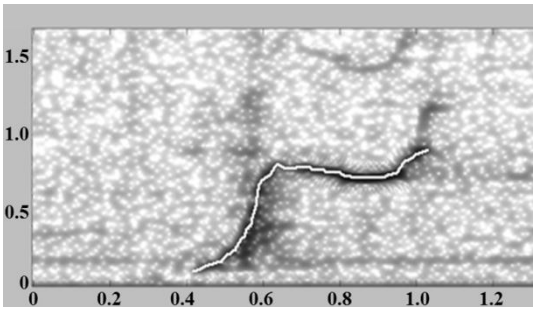
b) 

Figure 2.3 Spectrogram example of the Beluga contour tracing method, showing a) the tracing box around the signal and b) frequency contour trace

Additional measurements extracted from *Beluga* were: minimum frequency, maximum frequency, start frequency, stop frequency, duration, trend, and bandwidth (see Table 2.1 for full descriptions). Inflections, defined as changes in the slope of the frequency contour, were counted based on the extracted contour of the sound (following Dunlop *et al.*, 2007). Pulse repetition rate (PRR) was counted (per second) using the Raven spectrograms and corresponding waveforms from which these units were originally transcribed.

Table 2.1 Acoustic features measured for contoured units in *Beluga*.

Acoustic Feature	Definition
Max frequency (Hz)	Highest peak frequency extracted from the frequency contour
Min frequency (Hz)	Lowest peak frequency extracted from the frequency contour
Start frequency (Hz)	The first peak frequency extracted from the frequency contour
End frequency (Hz)	The last peak frequency extracted from the frequency contour
Trend	Start frequency/end frequency. Values >1 indicate a sound that decreases in frequency, while values <1 indicate a sound that increases in frequency
Duration (s)	Length of the unit based on the extracted frequency contour
Bandwidth (Hz)	Maximum frequency – minimum frequency
Inflection	Number of changes in the slope of the frequency contour
Pulse repetition rate (/s)	The number of pulses in sounds that are contoured but have a pulsative element
Contour point (x50) (Hz)	Subsamples of the peak frequency measurements taken every 0.03 seconds to create the frequency contour. 50 samples were taken, evenly spaced along the frequency contour. Each subsample was treated as its own acoustic feature

2.2.Non-contoured feature measurement

Non-contoured units were measured using the robust measurements available in Raven Pro 1.4 (Charif *et al.*, 2010). Recordings were imported into Raven as WAV files. Spectrograms of recordings were loaded with an FFT of 2048, Hann window, and 90% overlap. A tracing box was placed around units and the following features were extracted: duration, center frequency, peak frequency, frequency 5%, frequency 95%, and bandwidth 90% (Table 2.2). Inflection and pulse repetition rate (PRR) were counted visually based on the spectrogram and corresponding waveform.

Table 2.2 Acoustic features of non-contoured units measured using robust measurements in Raven

Acoustic Feature	Definition
Center frequency (Hz)	Frequency at which the sound is divided into two intervals of equal energy
Peak frequency (Hz)	Frequency at which the sound has maximum amplitude.
Frequency 5% (Hz)	Frequency at which the sound is divided into intervals containing 5% and 95% of its energy
Frequency 95% (Hz)	Frequency at which the sound is divided into intervals containing 95% and 5% of its energy
Duration (s)	Length of the unit based on the spectrogram visualization
Bandwidth 90% (Hz)	Frequency 95% - Frequency 5%
Inflection	Number of changes in the slope of the frequency contour
Pulse repetition rate (/s)	Number of pulses in sounds that have a pulsative element

2.3.4. Creating a self-organizing map

Self-organizing maps (SOM) were created using the *selforgmap* function of the Neural Network Toolbox in *MATLAB* 2014b. There were 59 acoustic features (9 variables and 50 frequency contour points) in the contoured input vectors, and 8 acoustic features in the non-contoured input vectors. Z-scores were used to standardize the data in order to account for the variety of different variable scales. Separate maps were created for the two types of signals due to the different methods of acoustic feature measurement described above (following Murray *et al.*, 2018). Map sizes that divide data too coarsely over-simplify differences, while dividing it too finely creates categories with superfluous detail (Walker *et al.*, 1996; Céréghino and Park, 2009). Map dimensions were therefore determined using trial and error (Kohonen, 2014). Due to the current study's aim of creating generalized sound types, 'lumping' signals into fewer broad groups was favored over 'splitting' them into many smaller ones that would not represent generalized

categories (Mercado and Kuh, 1998). The resulting dimensions were a 10 x 10 map (100 nodes) for contoured units and a 7 x 7 map (49 nodes) for non-contoured units. Once dimensions were established, the SOM was trained and created using the dataset, with neighborhood size and learning rate kept at the default MATLAB settings of 3 and 0.01 respectively (Demuth *et al.*, 2014). The chosen dimensions determined the number of nodes, or groupings into which the data were placed. Each measured signal was placed into a single node.

2.3.5. Comparison of SOM and qualitative classification

Classification and Regression Tree (CART) (Breiman *et al.*, 1984) and Random Forest (Breiman, 2001) analyses were used to assess the relative consistency between SOM and manual classification techniques when given the same set of data and input variables. Prior to the formation of the map, the measured sounds were also qualitatively assessed and classified by JA resulting in 261 contoured sound types and 42 non-contoured sounds. Agreement between the method of classification and the decision tree analyses were calculated for each classifying technique separately. Contoured and non-contoured units also had to be evaluated separately due to the differences in their acoustic variables. Multivariate PCA and DFA are commonly used analysis methods for corroboration of qualitative data categorization, particularly for animal vocalization (Boisseau, 2005; Dunlop *et al.*, 2007; Rekdahl *et al.*, 2013). However, CART analysis addresses assumptions made by these analyses; data can be non-parametric, non-normal, and have correlated variables (Van Opzeeland and Van Parijs, 2004; Melendez *et al.*, 2006; Garland *et al.*, 2012; Rekdahl *et al.*, 2013). CART decision trees split data into branches based on the Gini Index, a commonly used measure of "goodness of split" which reduces heterogeneity within the groups (Breiman *et al.*, 1984). At each split of the tree, all possible divisions to the data (by variable) are considered. This allows division of data to be based on a different splitting criterion at each branch (e.g., is start frequency > 500 Hz). The criterion chosen represents the highest reduction in heterogeneity in the data (Karels *et al.*, 2004). CART was implemented here with cross-validation using the *rpart* package in R (Therneau *et al.*, 2014), with each terminal branch of the CART (analogous to a node or a category) set to a minimum size of 10 (Table 2.3). Each of the resulting decision trees were pruned to prevent overfitting of the data using the 1-standard deviation rule (see Breiman *et al.*, 1984). CART provides information on the ability of the analysis to classify calls (root node error) and also the agreement in classification between CART and the classification technique it is evaluating.

Random Forest is a more robust expansion of CART, where a forest of CART trees is created to allow an internal estimate of uncertainty. By applying a bootstrapping technique known as 'tree bagging' to the process of creating decision trees, Random Forests can randomly sample combinations of the variables available to produce the lowest out-of-bag (OOB) error rate. This allows an estimate of classification error per call type and the overall OOB error rate of the forest, from which classification agreement can be determined. Random Forest was implemented here using the *randomForest* package in *R* (Table 2.3) (Liaw and Wiener, 2002), with 1000 trees grown for each forest and the predictor variables that were randomly selected set to 3. The Gini Index was also used here to indicate the importance of each of the predictor variables. Gini values indicate order of relative variable importance in the splitting decisions and are not directly comparable across separate analyses.

Table 2.3 Classification agreements between method of classification and decision tree analysis (both CART and Random Forest) used to evaluate classification techniques. Root node errors, determined for CART only, represents the percentage of classification of call types. Significantly higher agreements based on Mann-Whitney/Wilcoxon tests are shown in bold.

Corroborating Method	Unit Types	Qualitative Agreement	SOM Agreement
CART	Contoured	57.55%	73.03%
		(95.02% root node error)	(95.35% root node error)
CART	Non-contoured	78.97%	74.24%
		(93.20% root node error)	(81.11% root node error)
Random Forest	Contoured	73.01%	89.21%
Random Forest	Non-contoured	83.31%	90.93%

CART and Random Forest analyses were each used to evaluate the two classification techniques: 1) manual, or qualitative description (**Q**), and 2) SOM node placement (**SOM**). Contoured (**C**) and non-contoured (**NC**) units were analyzed separately given that they were measured differently. The dataset of contoured units was classified independently by both the SOM (**C-SOM**) and qualitatively (**C-Q**). The dataset of non-contoured units was also classified by both the SOM (**NC-SOM**) and qualitatively (**NC-Q**). Each of the four classifications was treated as a separate subset of the data. Each subset was evaluated separately for classification agreement with a CART analysis, as well as with a Random Forest analysis, for a total of eight analyses. A non-parametric Mann-Whitney/Wilcoxon test was used to compare the degree of classification agreement found for each method.

2.3.6. Utilizing SOM Cartesian distances to quantify song similarity

To quantify the relative acoustic similarities between prototype units, the distance between the nodes was measured on the Cartesian plane as arranged by the SOM spatial layouts (Fig. 2.4). Each SOM was placed on a two-dimensional plane and every node was assigned an (X,Y) coordinate with all adjacent nodes having a distance of 1. Based on these coordinates, a matrix was generated of all the relative Cartesian distances between the nodes in the SOM layout. This matrix provided a quantitative measurement of relative similarity among unit types based on their spatial arrangement in the SOM.

To demonstrate the utility of SOMs in combination with the similarity weightings, song cycles from the east Australian population in 2008 were transcribed following the prototype units generated from the SOM classification as a guide. Qualitatively identified themes within the 2008 song were then validated using Levenshtein distance analysis of the phrase repetitions transcribed using the SOM classifications. The Levenshtein distance is a similarity measurement that calculates the minimum number of insertions, deletions, and substitutions needed to convert one string of data into another. This score can then be normalized to account for differences in string length, creating an index of similarity known as the Levenshtein distance similarity index (LSI) (Helweg *et al.*, 1998; Garland *et al.*, 2012; Murray *et al.*, 2018). Here, a weighted LSI analysis was implemented where the cost matrix for substituting units was based on the matrix of Cartesian distances extracted from the SOM, exponentially scaled between 0 and 1. This allowed the cost of substituting similar units to be a direct measure of acoustic similarity and the cost of insertions or deletions remained as cost=1 (see Garland *et al.* (2017b) for detailed methodology and rationale). In essence, substitutions between highly similar units were considered to be less costly (based on SOM distances), while insertions, deletions, and substitution of units from separate maps were assigned a maximum penalty of cost=1. If themes that were qualitatively identified within the 2008 song could also be identified through the Levenshtein Distance analysis, it would demonstrate the repeatability of the transcriptions made using the acoustic dictionary. Average-linkage hierarchical cluster analysis and bootstrapping (using *pvclust* and *bootstrap* in *R*) were run to assess the similarity between all data strings. The cophenetic correlation coefficient (CCC) was also calculated as a measure of how accurately the above analyses represented the true similarity associations within the data, with a CCC>0.8 indicating a good representation of the data (Sokal and Rohlf, 1962).

2.4. Results

2.4.1. Creation of prototype units

From 76 song cycles and 3720 phrases, 6409 sound units were measured and placed in 149 SOM nodes, 100 nodes within a 10x10 contoured SOM and 49 nodes within a 7x7 non-contoured SOM. For each node, the average of each acoustic feature was calculated using all of the units placed in that particular node, creating feature vectors for a set of prototype units (Supplementary Materials, Table VI and VII). For the contoured SOM, each of the 50 frequency contour points within a node was averaged and graphed, creating a visual representation of the prototype unit for each node (Fig. 2.4). A visual representation of the non-contoured prototype units was not possible because there was no frequency contours to extract. Nodes were numbered from left to right, starting from the upper left node and ending with the lower right node. Prototype units were numbered 1-100 for contoured units based on their SOM node position, and from 101-149 for the non-contoured units. These units comprise an acoustic dictionary of sound units which represents the song repertoire from 2002-2014 for the east Australian humpback whale population.

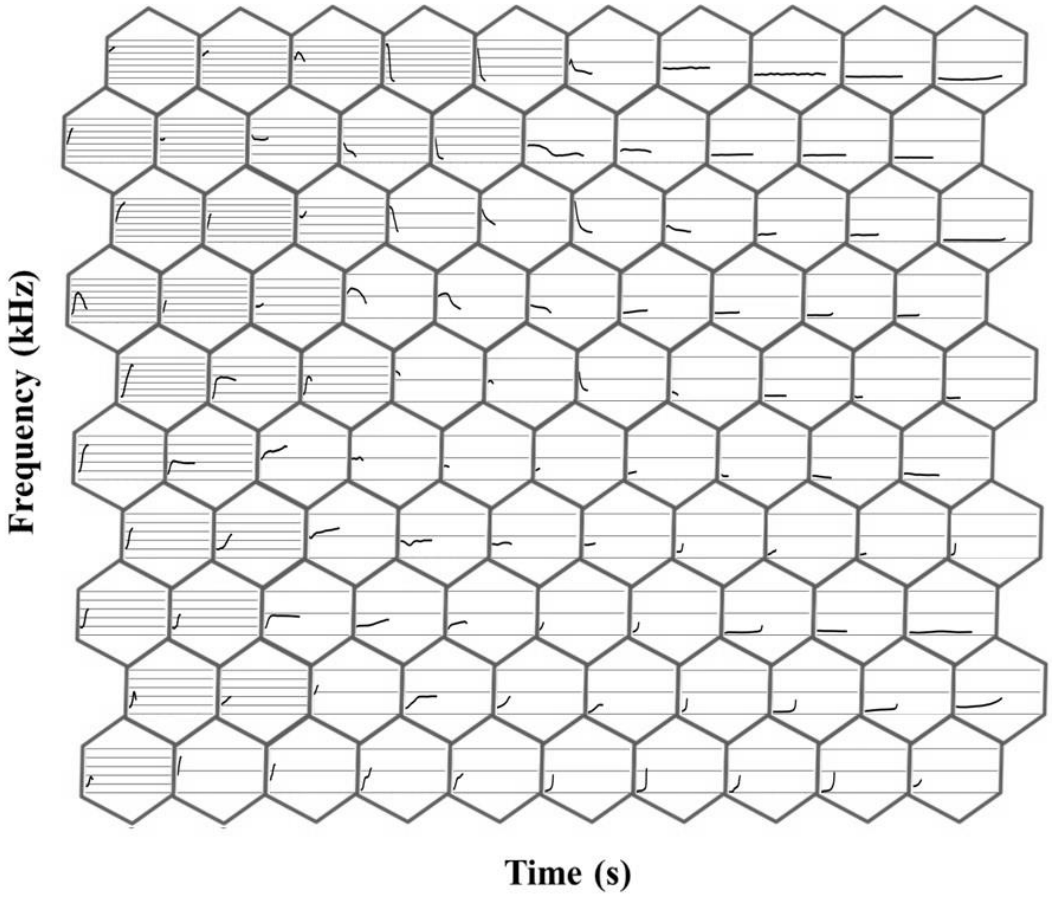


Figure 2.4 Visual representations of prototypical unit contours generated from the contoured unit 10 x 10 SOM, based on the 50 frequency contour points extracted using Beluga. All visual representations have time on the x-axis (5 seconds for all nodes) and frequency on the y-axis (gridlines represents one kilohertz intervals). Adjacent nodes are more similar to each other than those that are not adjacent.

2.4.2. CART analyses

For each of the CART analyses, a proportion of variables provided a root node error. This resulted in an agreement of classification between the classification technique (either qualitative or SOM) and the CART analysis. A summary of the classification agreements for each analysis can be found in Table 2.3. The top five variables used by the analyses and their respective Gini Index values in each analysis can be found in Table 2.4.

Table 2.4 Variables used in the CART analyses and mean decrease in Gini index. C-SOM = contoured units classified by SOM, C-Q = contoured units classified by qualitative naming, NC-SOM = non-contoured units classified by SOM, NC-Q = non-contoured units classified by qualitative naming.

CART							
C-SOM		**C-Q**		**NC-SOM**		**NC-Q**	
Variables	**Gini**	**Variables**	**Gini**	**Variables**	**Gini**	**Variables**	**Gini**
Duration	823	Duration	630	Freq. 95%	578	Duration	597
Trend	628	Trend	360	Bandwidth 90%	553	Center	439
Inflection	622	Start	344	Freq. 5%	434	Freq. 95%	413
End	469	Inflection	326	Center	418	Peak	410
Max	443	Contour Point 2	319	Peak	392	Freq. 5%	373

2.4.3. Random forest analyses

For each of the Random Forest analyses, agreement in classification between the classification technique (either qualitative or SOM) and the Random Forest analysis was reported, as well as the most important variables as assessed by the Gini Index. A summary of classification agreements for each analysis can be found in Table 2.4. The top five variables used by the analyses and their respective Gini Index values in each analysis can be found in Table 2.5.

Table 2.5 Variables used in the Random Forest analyses and mean decreasing Gini index. C-SOM = contoured units classified by SOM, C-Q = contoured units classified by qualitative naming, NC-SOM = non-contoured units classified by SOM, NC-Q = non-contoured units classified by qualitative naming.

RANDOM FOREST							
C-SOM		**C-Q**		**NC-SOM**		**NC-Q**	
Variables	**Gini**	**Variables**	**Gini**	**Variables**	**Gini**	**Variables**	**Gini**
Duration	805	Duration	821	Bandwidth 90%	330	Duration	416
Inflection	595	Trend	477	Freq. 95%	241	PRR	210
Trend	559	Inflection	342	PRR	224	Peak	197
Max	221	Max	188	Freq. 5%	218	Center	186
PRR	207	Bandwidth	179	Duration	217	Freq. 95%	155

2.4.4. Comparison of SOM and qualitative classification

Results of the comparison between SOM and qualitative classifications are summarized in Table 2.3. Classification agreement with the CART analysis was found to be significantly higher with the SOM technique (73%) as compared to the manual method (58%; Mann-Whitney/Wilcoxon, $W=4770.7$, $p<0.01$) for contoured units, but there was no significant difference in non-contoured units (Mann-Whitney/Wilcoxon, $W=918$, $p=0.48$). Classification agreement with the Random Forest analysis was found to be significantly higher with the SOM technique for both contoured (89% vs 73%; Mann-Whitney/Wilcoxon, $W=3987.5$, $p<0.01$) and non-contoured units (91% vs 83%; Mann-Whitney/Wilcoxon, $W=685$, $p<0.01$).

2.4.5. Utilizing the SOM prototypes and Cartesian distances to quantify song similarity

Using the SOM classifications, 36 complete song cycles of the 2008 song were transcribed from nine singers, comprising 7847 sound units arranged into 1864 phrases. No song cycles measured for the original SOM analyses were used in this analysis to ensure independent sampling. A dendrogram was generated based on LSI values using both hierarchical cluster analysis and bootstrapping to display similarity between phrases (Fig. 2.5). The cophenetic correlation coefficient (CCC) of 0.97 verified that the dendrogram was a very good representation of the associations within the dataset. Most phrase repetitions of a given qualitatively-identified theme were clustered together on the same major branch: therefore, each major branch represented a different theme. The exception was Theme D, which contained three phrase variants based on different phrase lengths (D1: two units, D2: three units, and D3: five units). A qualitative

examination of these variants (Fig. 2.5) showed that all three variants contained the same two starting units. For example, to create D2, the three-unit variant, one unit was inserted at the end of D1, the two-unit sequence. To create D3, the five-unit variant, two additional units were inserted to the end of D2 (the three-unit sequence). Differences in length are reflected in the LSI analysis, as insertions and deletions which lengthen or shorten a string were more heavily penalized in this weighted LSI framework than substitutions (Garland *et al.*, 2017b).

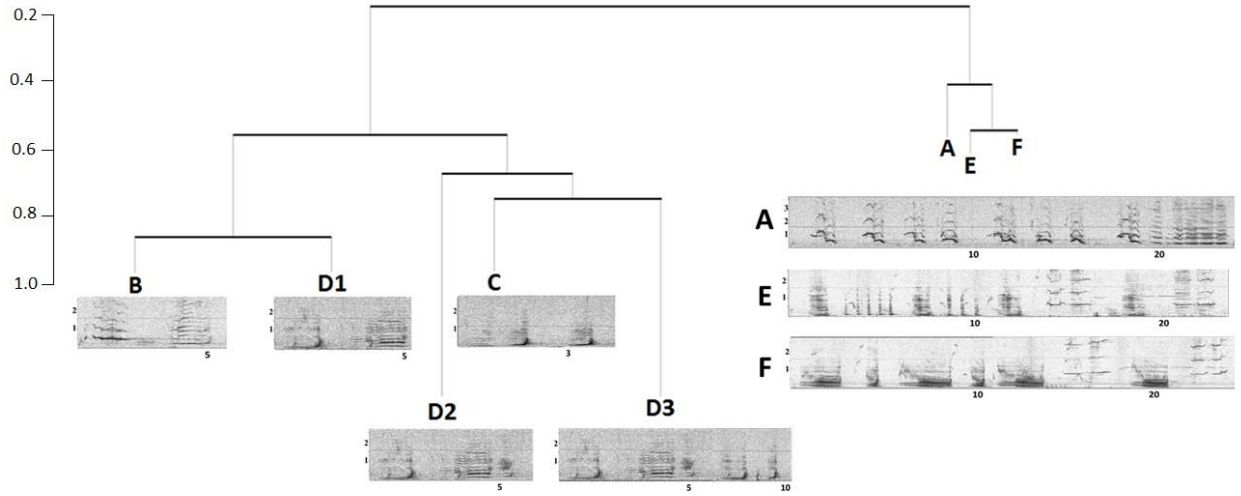


Figure 2.5 Average-linkage hierarchically bootstrapped dendrogram of the east Australian 2008 song based on the Levenshtein Similarity Index (LSI), which was weighted for substitutions using the Cartesian distances between units in the SOM. Horizontal lines correspond to the proportion of similarity, shown on the y-axis, between two branches. Each letter represents a qualitatively identified theme. Phrase repetitions of every theme, with the exception of Theme D, were clustered onto separate major branches. Spectrogram figures provide a visual representation of each theme, with time (s) on the x-axis and frequency (kHz) on the y-axis. Note that only major branches are shown; terminal branches representing individual phrase repetitions were excluded for clarity.

2.5. Discussion

SOM classification enabled the creation of an acoustic dictionary of prototypical units, which represents the repertoire of the east Australian humpback whale population's songs from 2002-2014. The Cartesian distances between those units, a valuable product of the SOM classification, provided a means of quantifying the similarity between all units across the entire dictionary, which can be utilized in higher-level sequence analyses (Garland *et al.* (2017b). This dictionary can serve as a guide by which vocal sequences from new recordings can be manually transcribed in a rapid, repeatable, and efficient manner. While prototypical units have been created to represent humpback whale song before (Walker *et al.*, 1996; Mercado and Kuh, 1998), small sample size in many of these studies limited their ability to be representative of an entire repertoire over multiple years. Furthermore, none quantified the acoustic similarities between their units.

Cartesian distances as unit similarity weightings were instrumental to the repeatability of the dictionary's application to a dataset. There will inevitably be variation in signal classification for manual transcriptions for sequences. Quantifying similarity across units allowed the Levenshtein Distance analysis to identify and cluster repetitions of a specific theme despite those variations. The splitting of one theme's variations onto several branches based on length and unit types reveals the important role that qualitative judgment still plays in the classification and analysis of sequences. Ultimately a dictionary can minimize the amount of work needed to analyze large volumes of data; it requires only a relatively small subset of acoustic signals to be individually measured. Given that acoustic databases can contain hundreds of hours of recordings, comprehensive analyses can be difficult if every unit must be measured. Measuring a representative subsample to create a dictionary should increase the sample size of recordings that could ultimately be used for further analysis in many types of vocalization studies.

Precedence exists for SOM signal classification in a number of species, and it has some advantages over the manual technique. Although entirely automatic techniques would be the most objective, vocal signals often have too much variation for these to be effective (Janik, 1999). SOM classification eliminates one of the many qualitative steps within the study of vocalizations by placing signals into categories through quantitative and repeatable means. Map size is subjectively derived, but an advantage of this is that it allows for flexibility in studies of vocalizations at different resolutions. Small maps can be used for broad-scale contexts like territories or inter-population variation, while larger maps can be used for fine-scale detail such as individual variation. When implementing the dictionary on new, unmeasured recordings, the prototype unit that is ultimately selected as the best match for a signal is still manually decided. The similarity weightings derived from the SOM account for the variations in manual classification that occur due to subtle differences or similarities in unit types that may be identified by the human observer.

CART and Random Forest analyses provided a quantitative means of directly comparing between SOM and manual classification techniques. Both analyses found significantly higher classification agreement when contoured units were classified by the SOM method as compared to being classified manually. While Random Forest also found significantly higher agreement when non-contoured units were classified by the SOM, there was no significant difference in classification agreement when non-contoured units were classified either SOM or manually. This implies that the SOM method is more effective for contoured sounds. Acoustic characteristics can impact which technique might be better suited to each signal type. Subtle differences in the contour

of tonal sounds may be obscured to a human observer, particularly in cases of repetitive sequences with gradually changing units. Conversely, acoustic measurements of non-contoured units may not necessarily create a comprehensive description of the signal. It should be noted, however, that biological relevance of these differences in either signal type is unclear. A disadvantage of the SOM is that human observers can often detect nuanced differences not captured by measurement alone, which is why automatic classification has typically been less accurate (Janik, 1999). This could explain why CART found the SOM and manual techniques to be equivalent for non-contoured units. Manual classification has the advantage of recognizing and addressing these nuanced differences, while SOM has the advantage of being a more repeatable and robust approach.

The methods described here are only applicable to high-quality recordings from which acoustic features can be measured accurately. The subset of recordings measured must also be representative of the dataset under analysis. Additionally, the use of a single singer in each year does not consider individual variations. This represents a limitation of the method as applied to this dataset, and should be taken into account whenever appropriate during use in future studies. Using data that fit the described criteria, acoustic similarity and structure of vocal signals can be quantified for any number of vocal databases. Furthermore, an acoustic dictionary could also be generated for these databases, filling a current gap in the body of knowledge (Placer *et al.*, 2006; Kaufman *et al.*, 2012). This dictionary could then be used as a guide to transcribe sequences in new recordings from the respective population or database. Quantifiable similarity between these prototypical units can enhance the repeatability of the dictionary's application when used in subsequent sequential analyses. While this method by no means eliminates the limitations of the traditional approaches to acoustic signal categorization and analysis, it does provide a key step in the process towards a more quantitative, robust, and repeatable approach.

***See supplementary material for Tables VI and VII, which provide the averages for each of the acoustic feature variables used in the 10x10 contoured SOM (Table 2.6) and the 7x7 non-contoured SOM (Table 2.7).**

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2.7. Supplementary Materials

Table 2.6 Average values (± standard deviation) for all acoustic feature variables used in the 10 x 10 contoured units SOM. The averages for each of the 50 frequency contour points are not listed here.

Node	max frequency	min frequency	start frequency	end frequency	trend	Duration	Bandwidth	Inflection	PRR
1	6017.51±415.32	5122.87±433.56	5270.45±467.46	5894.12±461.15	0.9±0.11	0.33±0.21	894.65±613.37	2.12±1.72	0±0
2	5402.57±272.45	4341.83±424.13	4656.49±443.12	5219.76±386.1	0.9±0.11	0.34±0.19	1060.75±510.39	2.44±1.5	0±0
3	5397.14±398.72	3443.31±450.98	4179.97±531.57	3734.3±596.96	1.16±0.28	0.61±0.2	1953.83±635.44	4.54±2.19	0±0
4	6554.71±1055.93	460.81±10.55	6317.19±1028.09	493.65±29.79	12.85±2.33	0.48±0.04	6093.9±1052	0.6±0.49	0±0
5	4057.81±577.72	435.45±107.32	3976.54±558.45	445.53±97.68	9.27±1.74	0.44±0.09	3622.36±484.35	0±0	0±0
6	1173.1±203.69	461.55±54.57	978.16±102.63	479.14±59.92	2.06±0.25	1.35±0.29	711.54±182.6	4.43±1.43	0±0
7	886.75±157.17	546.31±98.9	728.3±84.98	747.36±178.72	1.03±0.25	2.79±0.78	340.43±197.21	7.62±1.7	0±0
8	558.52±240.59	370.1±97.78	435.33±149.36	471.47±174.06	0.94±0.14	4.26±0.43	188.42±179.72	16.19±1.67	0±0
9	389.33±127.81	304.59±106.66	348.91±118.44	350.92±121.51	1.01±0.15	3.34±0.41	84.74±47.43	10.26±1.44	0±0
10	402.25±282.84	168.94±90.76	260.12±120.82	360.53±278.54	0.88±0.3	3.8±0.56	233.3±293.19	5.02±1.34	0.87±4.08
11	5469.93±571.24	3039.06±531.87	3092.36±526.46	5431.2±575.38	0.58±0.12	0.33±0.17	2430.87±882.13	1±1.17	0±0
12	3973.44±334.45	3539.5±242.75	3769.92±385.35	3821.11±290.03	0.99±0.13	0.25±0.16	433.94±358.6	2.34±2.04	0±0
13	3331.51±381.64	2442.52±283.19	3026.51±431.18	2798.72±374.85	1.1±0.19	0.95±0.31	888.98±399.8	3.33±1.65	0±0
14	2258.36±202.62	718.86±97.13	2179.04±243.72	750.69±98.59	2.94±0.45	0.73±0.32	1539.49±204.96	1.91±1.53	0±0
15	2868.45±450.53	469.2±63.1	2557.7±515.39	630.48±719.45	5.48±1.35	0.45±0.1	2399.25±403.53	0.16±0.49	0±0
16	898.41±132.22	209.95±48.58	795.92±131.32	335.12±82.16	2.55±0.84	3.33±0.31	688.46±115.6	3.67±1.37	0±0
17	684.05±69.01	431.9±88.69	559.99±126.73	498.81±87.51	1.15±0.29	1.81±0.38	252.15±93.67	4.44±1.19	0±0
18	410.44±74.13	314.33±55.4	348.16±53.82	374.49±76.97	0.95±0.13	2.47±0.43	96.11±58.29	6.2±1.01	0±0
19	380.43±85.89	295.41±72.96	326.99±62.02	341.03±90.07	0.99±0.16	2.52±0.43	85.02±62.95	3.06±0.79	0±0
20	264.58±45.53	221±42.52	248.22±39.55	231.91±45.26	1.1±0.21	2.26±0.31	43.59±44.51	0.58±0.66	0±0
21	6487.47±484.62	3266.77±569.08	3405.89±532.49	6365.93±566.48	0.54±0.09	0.53±0.14	3220.71±609.36	1.57±1.65	0±0
22	4456.09±565.47	2114.93±545.32	2129.26±537.91	4443.16±558.65	0.48±0.1	0.21±0.06	2341.15±505.64	0.25±0.56	0±0

23	3573.19±358.87	2694.01±214.73	3005.2±409.49	3451.31±364.46	0.88±0.17	0.38±0.36	879.18±435.47	1.09±0.95	0±0
24	2652.38±386.06	766.33±245.3	2342.6±605.84	903.73±532.32	3.19±1.35	0.48±0.19	1886.06±450.96	2.88±2	0±0
25	1507.23±197.57	819.06±113.76	1473.11±179.63	832.43±106.88	1.8±0.3	0.75±0.44	688.17±211.32	0.45±0.75	0±0
26	1879.37±212.05	461.17±46.62	1762.25±202.8	469.53±44.43	3.77±0.41	0.41±0.09	1418.2±204.23	0.08±0.28	0±0
27	814.07±127.3	474±57.39	742.63±132.71	492.22±56.83	1.52±0.29	1.42±0.31	340.07±139.53	1.07±0.83	0±0
28	451.16±69.1	309.77±46.85	338.96±50.29	400.98±81.66	0.87±0.18	1.05±0.32	141.38±74.84	2.82±0.72	0±0
29	379.21±104.27	255.87±55.34	290.54±53.92	318.87±93.78	0.96±0.22	1.66±0.34	123.34±91.2	4.58±0.58	0±0
30	188.77±57.9	93.31±39.44	108.97±59.98	146.69±46.92	0.74±0.19	3.69±0.56	95.46±27.2	0.13±0.34	0±0
31	4979.14±760.43	1318.49±491.7	1408.08±554.43	2327.25±647.29	0.65±0.28	0.89±0.3	3660.64±874.48	1.62±0.92	0±0
32	3479.33±453.14	1651.6±261.45	1683.93±266.6	3451±457.51	0.49±0.09	0.17±0.04	1827.74±496.16	0.96±1.15	0±0
33	2291.78±363.3	1715.14±192.63	1832.49±324.71	2149.31±413.58	0.88±0.19	0.44±0.42	576.64±313.05	1.24±1.6	0±0
34	1456.66±147.78	667.74±140.63	1181.98±230.95	715.22±149.69	1.73±0.49	1.12±0.44	788.92±194.97	1.8±1.05	0±0
35	1202.27±155.02	433.8±47.59	1033.16±162.14	447.26±47.2	2.35±0.54	1.3±0.54	768.47±169.78	1.9±1.23	0±0
36	621.87±100.39	247.38±58.2	595.73±93.7	264.46±54.95	2.29±0.31	1.2±0.38	374.49±70.53	1.18±1.08	0±0
37	411.73±94.03	225.69±67.95	241.02±69.96	343.8±100.31	0.71±0.13	1.42±0.21	186.04±82.89	0.83±0.47	0±0
38	304.55±94.39	206.82±51.42	242.57±58.09	260.11±78.99	0.96±0.2	1.44±0.23	97.72±77.6	2.43±0.49	0±0
39	225.09±99.21	146.96±70.64	176.5±77.83	193.4±90.99	0.96±0.26	1.52±0.35	78.13±65.36	3.37±0.9	0±0
40	161.2±91.19	102.48±55.64	110.22±56.34	140.39±78.42	0.84±0.22	1.28±0.21	58.72±63.78	0.44±0.51	0±0
41	6032.37±811.43	775.96±67.42	837.55±106.43	5760.01±737.88	0.15±0.02	0.72±0.14	5256.41±839.78	1.43±1.24	0±0
42	3033.79±553.91	414.19±241.09	555.09±261.89	2483.62±184.43	0.22±0.11	1.39±0.25	2619.59±653.04	5.29±1.75	0±0
43	2650.54±758.63	858.39±251.04	890.06±245.79	2206.93±776.21	0.5±0.28	0.48±0.21	1792.15±564.01	0.91±0.67	0±0
44	1498.14±148.15	1175.71±153.89	1393.9±184.02	1267.06±199.84	1.13±0.26	0.23±0.22	322.43±207.86	1.58±1.22	0±0
45	1081.71±174.87	803.84±136.25	925.8±204.45	891.91±139.15	1.05±0.23	0.28±0.32	277.87±190.16	0.96±0.68	0±0
46	1354.78±223.9	490.63±105.17	1227.01±196.41	505.72±108.18	2.47±0.44	0.49±0.4	864.14±207.51	0.46±0.64	0±0
47	435.69±50.04	267.48±53.41	391.7±63.91	278.14±50.34	1.44±0.26	0.83±0.31	168.21±63.01	0.84±0.55	0±0
48	271.09±43.24	216.05±41.88	247.62±44.72	234.78±42.3	1.07±0.15	1.26±0.22	55.04±42.34	0.66±0.47	0±0

49	239.58±63.88	156.43±42.85	213.37±49.43	186.18±42.54	1.17±0.23	0.43±0.23	83.16±64.35	3.59±1.17	0±0
50	191.19±46.45	112.25±37.94	161.54±44.12	148.82±43.86	1.11±0.22	0.8±0.2	78.94±41.66	1.42±0.49	0±0
51	4045.71±478.52	894.89±242.33	938.86±223.58	3949.6±536.33	0.24±0.06	0.58±0.23	3150.81±555.74	1.47±1.09	0±0
52	2300.96±305.05	705.72±268.04	856.35±194.72	1902.71±269.41	0.46±0.13	1.59±0.43	1595.24±377.58	5.07±2.07	0±0
53	1595±204.78	916.13±208.59	973.76±187.4	1519.68±173.56	0.65±0.14	1.53±0.27	678.88±279.32	2.44±1.22	0±0
54	1155.45±132.04	786.46±183.46	970.43±160.97	910.17±228.28	1.14±0.35	0.67±0.51	368.99±255.59	4±1.13	0±0
55	711.46±79.8	531.16±87.91	629.22±81.06	597.54±133.69	1.1±0.26	0.28±0.2	180.3±96.34	1.27±0.75	0±0
56	541.48±84.38	423.43±78.79	447.76±87.26	515.83±83.92	0.87±0.13	0.22±0.13	118.05±72.66	0.75±0.73	0±0
57	373.62±62.09	268.92±47.89	278.79±48.96	356.91±58.35	0.79±0.13	0.46±0.25	104.71±59.86	0.68±0.67	0.23±2.12
58	245.69±47.65	158.04±33.07	236.01±45.69	171.39±36.35	1.4±0.21	0.39±0.14	87.65±37.04	0.74±0.59	0±0
59	191.06±47.4	83.61±21.27	172.92±49	86.6±20.66	2.02±0.39	1.11±0.34	107.45±39.52	0.35±0.62	0±0
60	236.39±76.6	63.17±36.83	195.55±89.87	71.25±42.1	3.17±1.49	2.07±0.46	173.22±49.41	0.96±0.52	0±0
61	3408.55±290.56	1035±195.14	1112.54±180.51	3321.11±275.06	0.34±0.06	0.4±0.3	2373.55±373.77	1.03±0.93	0±0
62	2694.31±234.78	953.39±119.61	1007.96±130.2	2650.01±223.48	0.38±0.05	0.9±0.63	1740.92±246.63	1.27±1.35	0±0
63	1380.47±160.38	869.72±132.71	918.43±131.35	1354.48±147.7	0.68±0.09	1.75±0.28	510.75±168.77	5.53±1.52	0±0
64	887.59±89.99	497.36±58.36	763.07±74.46	796.79±87.63	0.97±0.14	1.84±0.37	390.22±107.48	4.32±1.11	0±0
65	745.55±90.55	548.82±106.74	638.22±94.54	647.06±113.71	1±0.15	1.15±0.23	196.74±144.84	1.99±0.83	0±0
66	721.85±80.1	537.36±81.53	603.19±81.52	660.22±104.16	0.94±0.22	0.62±0.33	184.49±101.53	4.62±1.24	0±0
67	629.54±101.15	252.11±36.64	280.06±45.5	602.7±90.84	0.47±0.07	0.38±0.19	377.42±91.64	1.56±0.78	0±0
68	415.79±112.42	146.84±42.4	155.96±45.02	347.73±93.44	0.45±0.07	0.48±0.22	268.95±110.07	0.79±0.67	0±0
69	204.24±31.94	144.84±27.92	150.77±26.33	198.95±29.46	0.76±0.12	0.34±0.13	59.4±33.03	0.18±0.38	0±0
70	653.79±146.09	137.68±65.11	155.22±59	561.55±135.96	0.29±0.12	0.64±0.38	516.11±159.7	0.87±0.83	45.15±9.99
71	2998.99±327.71	849.57±122	966.28±215.88	2955.53±341.92	0.33±0.06	0.49±0.07	2149.42±283.91	1.94±1.26	0±0
72	2342.05±289.61	771.49±89.43	864.98±138.08	2319.45±287.12	0.38±0.1	0.47±0.06	1570.56±331.89	2.67±1.58	0±0
73	933.7±96.55	346.33±182.34	414.49±173.99	854.9±92.76	0.48±0.15	2.03±0.51	587.38±146.01	1.17±0.37	0±0
74	767.11±143.59	348.77±71.83	418.27±84.87	712.42±129.6	0.61±0.17	1.9±0.47	418.34±180.12	2.02±0.91	0±0

75	643.82±88.6	287.4±84.39	333.01±67.39	569.75±109.63	0.59±0.11	1.08±0.3	356.41±99.6	1.09±0.6	0±0
76	569.97±82.55	254.54±36.4	259.54±37.32	559.08±81.03	0.47±0.08	0.23±0.12	315.43±81.46	0.22±0.41	0±0
77	585.21±125.28	149.38±33.21	157.22±34.85	531.29±106.6	0.3±0.04	0.35±0.21	435.83±110.27	0.17±0.46	0±0
78	428.52±210.68	96.66±30.5	117.39±36.79	286.15±87.34	0.42±0.08	2.21±0.29	331.86±195.3	1.75±1.32	0±0
79	238.51±90.67	151.31±76.7	210.18±92.69	181.73±71.83	1.16±41.84	1.73±0.54	87.2±38.33	2.16±1.42	29.05±4.9
80	216.57±91.57	99.8±25.44	129.67±31.77	145.22±42.4	0.94±0.23	3.69±0.68	116.78±81.98	2.23±1.72	29.23±4.27
81	2574.92±126.11	761.6±53.07	773.83±57.21	1696.68±257.14	0.46±0.06	0.41±0.04	1813.32±135.03	1.53±0.82	0±0
82	1980.29±199.29	1128.19±226.07	1137.44±230.74	1960.06±191.25	0.58±0.12	0.53±0.54	852.1±256.95	0.36±0.81	0±0
83	1307.82±144.97	887.96±67.83	917.17±105.56	1288.06±147.61	0.72±0.09	0.23±0.26	419.86±152.29	0.5±0.76	0±0
84	853.55±128.18	243.31±55.95	286.41±46.7	809.26±81.67	0.35±0.05	1.83±0.26	610.24±143.35	1.11±0.85	0±0
85	790.05±94.84	288±56.34	304.21±52.81	776.76±92.58	0.4±0.08	0.75±0.32	502.06±104.82	0.59±0.77	0±0
86	479.34±82.68	76.92±20.68	82.63±22.43	419.46±86.07	0.2±0.04	0.84±0.25	402.42±72.1	1.27±0.59	0±0
87	689.24±151.26	122.65±31.72	129.25±31.62	631.24±141.84	0.2±0.02	0.3±0.19	566.58±129.2	0.03±0.17	0±0
88	633.09±278.36	87.61±24.98	104.29±27.31	396.01±89.42	0.27±0.06	1.34±0.28	545.48±277.17	0.57±0.68	0±0
89	450.95±171.43	126.75±40.69	149.47±36.84	342.52±75.59	0.44±86.53	1.91±0.41	324.2±190.04	1.1±0.99	27.5±5.04
90	738.25±146.67	292.38±48.85	332.29±65.04	683.92±142.56	0.52±0.22	2.73±0.7	445.86±118.03	2.17±1.72	50.43±5.9
91	1894.66±146.22	745.02±63.95	774.15±75.6	1585.37±148.78	0.49±0.05	0.4±0.12	1149.64±166.62	1.5±0.82	0±0
92	1644.02±132.16	808.88±112.57	821.7±112.28	1633.11±138.73	0.5±0.07	0.2±0.11	835.14±139.62	0.26±0.52	0±0
93	1237.38±304.15	518.54±133.51	531.99±139.31	1172.87±359.96	0.47±0.07	0.29±0.16	718.84±217.2	0.44±0.68	0±0
94	1127.42±254.73	114.74±29.34	127.03±29.91	1104.16±246.63	0.12±0.02	0.6±0.13	1012.68±232.52	1.26±0.97	0±0
95	878.13±119.89	162.81±39.94	176.54±35.55	851.54±125.86	0.21±0.04	0.55±0.19	715.33±108.17	0.93±0.92	0±0
96	813.6±261.25	82.57±15.63	86.89±15.4	630.07±108.98	0.14±0.01	0.48±0.29	731.03±258.44	0.04±0.2	0±0
97	1098.19±206.93	71.06±10.98	72.21±11.66	791.49±138.82	0.09±0.01	0.58±0.21	1027.13±204.29	0±0	0±0
98	760.94±154.17	23.98±1.73	28.18±6.97	713.99±184.77	0.04±0	0.26±0.09	736.95±152.75	0.67±0.94	22.22±15.95
99	926.32±406.32	53.56±20.01	67.28±20.1	684.32±161.12	0.1±0.02	0.75±0.32	872.76±398.02	0.33±0.62	42.78±8.59
100	592.83±139.35	290.65±133.38	314.92±145.5	569.46±140.93	0.57±0.26	0.47±0.55	302.18±162.96	1.28±1.33	76.48±10.63

Table 2.7 Average values (± standard deviation) for acoustic feature variables used in the 7 x 7 non-contoured units SOM.

Node	Center Freq	Peak Freq	Freq 5%	Freq 95%	Duration	Bandwidth 90%	Inflection	PRR (/s)
101	3045.07±209.11	2981.39±218.47	2818.97±203.42	3427.51±238.15	0.2±0.09	608.54±207.09	0±0	20.72±5.89
102	1378.56±129.14	1446.18±160.47	990.96±169.77	1831.2±254.82	0.39±0.5	840.24±224.49	0±0	3.2±5.29
103	848.03±64.87	829.03±110.78	689.07±70.74	986.1±60.35	0.72±0.13	297.03±82.74	0±0	58.63±7.26
104	392.66±60.02	390.76±72.53	323.01±37.67	465.51±71.57	1.11±0.53	142.5±47.51	0±0	19.02±8.15
105	469.95±101.04	468.82±102.84	435.2±84.89	523.79±117.96	0.19±0.03	88.59±46.69	0±0	0.18±1.31
106	357.51±59.73	351.43±62.05	304.51±44.83	438.13±80.75	0.43±0.29	133.62±43.86	0±0	0±0
107	116.82±29.74	117.35±24.99	97.99±26.14	165.28±44.95	0.44±0.08	67.29±22.02	0±0	0±0
108	1337.75±87.43	1317.57±93.55	1162.81±116.77	1461.58±96.71	0.31±0.4	298.77±114.92	0±0	0±0
109	696.61±57.79	700.91±70.62	536.18±75.38	919.84±104.85	0.55±0.3	383.66±94.09	0±0	17.11±5.69
110	492.94±55.43	476.96±90.06	273.11±34.44	841.6±104.65	0.42±0.21	568.48±90.23	0±0	22.03±5.03
111	466.96±78.66	461.43±99.42	285.16±56.82	634.93±99.69	0.77±0.33	349.77±75.93	0±0	14.33±4.72
112	318.26±44.02	305.11±44.75	259.49±26.72	518.07±79.79	0.44±0.15	258.58±67.27	0±0	0±0
113	95.3±22.44	92.91±23.64	73.77±19.83	159.5±41.45	0.46±0.1	85.73±22.58	0±0	0±0
114	131.79±22.01	123.42±25.27	102.48±15.89	267.97±44.09	0.32±0.11	165.49±30.47	0±0	0.93±3.98
115	1062.46±126.11	1003.45±87.59	910±87.37	1388.46±155.32	0.48±0.49	478.46±141.87	0±0	0±0
116	908.62±139.95	899.72±176.26	584.68±169.51	1396.86±268.21	0.58±0.39	812.17±177.91	0±0	4.49±6.32
117	507.53±69.46	447.4±116.13	263.18±35.21	1213.94±137.7	0.33±0.18	950.76±129.29	0±0	20.79±5.62
118	496.8±117.27	583.33±124.17	149.58±53.93	1082.44±196.27	0.22±0.1	932.86±164.17	0±0	1.79±3.83
119	560.1±78.61	567.51±118.85	249.3±58.83	907.99±115.15	0.43±0.27	658.69±82.1	0±0	10.11±4.55
120	333.06±57.52	344.54±82.21	157.53±61.99	701.47±157.07	0.26±0.11	543.95±115.97	0±0	0.82±2.66
121	122.72±39.29	111.75±35.74	83.74±22.24	315.62±77.23	0.35±0.11	231.87±57.95	0±0	0±0
122	1082.03±132.71	1059.8±186.76	607.24±191.09	2009.55±337.15	1.95±0.61	1402.32±302.63	0±0	0±0
123	753.34±142.23	650.81±159.99	469.92±93.29	1780.54±250.8	0.54±0.37	1310.62±256.15	0±0	19.42±7.95
124	526.71±104.1	392.12±134.39	239.71±32.45	1647.01±156.91	0.22±0.19	1407.3±166.72	0±0	12.59±5.24
125	258.52±96.58	183.75±78.41	106.71±28.57	1144.5±150.9	0.28±0.13	1037.78±145.76	0±0	0.11±1.05
126	181.4±62.74	125.62±74.72	78.29±29.91	685.15±106.22	0.29±0.1	606.86±94	0±0	0±0
127	99.53±36.23	82.61±41.63	35.4±18.05	261.73±130.03	0.51±0.18	226.33±123.85	0±0	32.63±6.26
128	106.38±43.43	95.44±46.46	53.1±21.88	334.67±94.08	0.41±0.11	281.57±79.42	0±0	0±0
129	1148.12±171.47	1086.2±231.21	544.61±219.7	2575.86±294.9	0.88±0.29	2031.25±229.55	0±0	2.08±8.15
130	1052.48±243.56	441.77±160.35	340.47±113.29	2583.62±426.86	1.35±0.48	2243.15±401	0±0	0±0
131	159.96±65.2	126.11±37.14	59.99±9.73	2157.94±213.83	0.44±0.14	2097.96±215.86	0±0	0±0
132	587.22±196.67	566.32±182.66	327.42±65.43	1232.15±208.24	1.64±0.61	904.73±180.87	0±0	0.98±3.92
133	270±70.98	241.82±85.58	121.75±37.16	1051.83±164.07	0.64±0.25	930.08±175.9	0±0	31.15±6.96
134	150.56±63.32	122.03±81.51	64.78±19.51	316.18±75.9	1.4±0.28	251.4±64.8	0±0	22.78±3.95
135	200.97±110.45	197.38±115.08	138.17±117.05	337.35±74.78	2.07±2.38	199.18±67.17	1±0	39.44±12.08
136	1287.97±108.53	1203.85±319.94	454.89±79.54	3652.56±439.06	1.24±0.3	3197.68±441.88	0±0	0±0
137	947.46±108.09	969.02±103.72	292.86±85.72	2368.64±353.31	3.76±0.51	2075.78±324.76	0±0	0±0

138	296.26±152.92	258.81±132.95	193.02±75.9	1504.26±177.4	3.8±0.42	1311.24±228.27	0±0	25.27±14.54
139	265±77.93	198.69±126.14	80.26±38.43	508.73±164.71	2.56±0.33	428.47±142.43	0±0	19.7±3.88
140	323.68±42.66	304.16±40.73	228.8±40.92	475.77±55.97	2.09±0.5	246.97±36.4	0±0	22.08±5.76
141	103.18±14.53	94.9±23	62.97±10.9	163.78±26.69	1.04±0.21	100.81±21.12	0±0	36.82±6.05
142	89.74±30.23	85.23±44.62	51.19±16.54	207.21±117.19	0.52±0.21	156.02±117.73	0±0	69.72±12.13
143	1354.82±336.4	748.29±563.79	331.98±111.71	5851.66±596.31	1.2±0.33	5519.68±543.51	0±0	0±0
144	793.51±189.48	630.92±308.48	202.4±146.91	2264.22±434.17	3.73±0.3	2061.82±388.89	0±0	76.67±9.55
145	741.84±452.57	393.32±327.44	230.57±107.81	2266.98±565.78	5.16±0.74	2036.41±506.83	0±0	41.88±3.9
146	619.64±362.43	611.62±335.91	439.39±177.58	788.18±452.01	5.23±0.71	348.79±283.72	0±0	36.3±5.08
147	345.89±19.73	329.73±22.16	292.05±6.47	410.48±40.1	5.54±1	118.43±36.52	2.5±0.5	26.25±4.23
148	204.1±91	206.44±90.72	161.03±91.66	251.83±114.73	2.28±0.42	90.8±33.44	0±0	45.07±7.54
149	210.79±39.73	208.53±57.54	78.76±23.45	283.32±14.43	2.72±0.18	204.56±20.38	0±0	50.88±6.56

CHAPTER 3 Temporal changes in humpback whale song complexity suggests a limit to social learning capacity

3.1 Abstract

Vocally learned displays, such as the songs of birds and cetaceans, are important components of non-human culture. While complexity of songs in many birds is associated with male fitness, complexity of songs in humpback whales (*Megaptera novaeangliae*), which may serve a similar function, has received less attention. All males in a population of humpback whales conform to the same song at any one time, but the song evolves from year to year. The east Australian population is unusual, however, in that every two to three years, their song is completely replaced in cultural 'revolutions' which involve learning large amounts of novel material introduced from the west Australia. We hypothesized that revolutions will result in a song with a lower complexity, due to a number of constraints on humpback whale learning ability. We examined song complexity and entropy in the east Australian population over 13 consecutive years. Given the song's hierarchical structure, complexity was quantified each year at two levels: the entire sequence of individual sound 'units' making up the song, and the stereotyped arrangements of units, comprising a 'theme'. Complexity scores were generated from six variables representing these two levels using principal component analysis (PCA). Complexity increased as songs evolved over time, but decreased when revolutions occurred. Changes in song complexity were from a combination of changes at both levels (unit and theme sequences) within the song. No correlation was found, however, between complexity and the second-order entropy estimates of either unit or theme sequences, revealing that predictability remained relatively stable. Changes to complexity may therefore represent embellishment to song arrangements rather than changes to potential information content. Together with the correlation that complexity demonstrates with revolution events, this suggests that while song structure and message are retained, there may be an upper limit to the capacity of social learning in humpback whales.

3.2 Introduction

Cultural transmission of behaviour in non-human species has become a provocative topic (Rendell and Whitehead, 2001). Culture itself is broadly defined as a behaviour or trait that is shared between individuals or conspecifics through their social ties (Rendell and Whitehead, 2001; Whiten, 2009). This type of learning, known as 'social learning', occurs through individual associations within a group (Galef, 1992; Heyes, 1994). Examples of non-human cultural learning include the spread of sweet potato washing in Japanese macaques (*Macaca fuscata*) (Kawai, 1965), the sponging foraging strategy of a small group of bottlenose dolphins (*Tursiops truncates*) in Western Australia (Krützen *et al.*, 2005; Kopps and Sherwin, 2012), and innovative string-pulling by bumblebees (*Bombus terrestris*) (Alem *et al.*, 2016). Understanding culture and social learning across a variety of species provides a comparative framework for the evolutionary role of culture in both animals and humans (Galef, 1992; Rendell and Whitehead, 2001; Laland and Janik, 2006; Whiten, 2009; Claidière and Whiten, 2012).

An important focus in non-human cultural studies is how vocal learning and communication may produce and maintain cultural traits (reviewed by Laland and Janik (2006)). Vocal learning typically refers to instances where vocal signals are produced or modified due to experiences with other individuals (Janik and Slater, 2000). Birdsong dialects (Slater, 1986), geographic differences in vocal patterns observed between adjacent populations (Marler and Tamura, 1962), demonstrate a result from such 'vocal production learning'. Mammalian examples include maternally-influenced echolocation calls in greater horseshoe bats (*Rhinolophus ferrumequinum*) (Jones and Ransome, 1993), cases of vocal imitation in African savannah elephants (*Loxodonta africana*) (Poole *et al.*, 2005), and culturally transmitted dialects based on maternal lineage in killer whales (*Orcinus orca*) (Deecke *et al.*, 2000). Complexity in the features of different vocal learning displays fall along a broad gradient (Janik and Slater, 2000). Where a display fits on this spectrum of complexity can provide insight into the learning mechanisms, motivations, or function behind the display.

Quantifying complexity in vocal displays is not straightforward. Song displays of species such as birds and cetaceans are considered more 'complex' than most vocal displays because of their sequential arrangements, yet do not reach the levels of complexity seen in human language (van Heijningen *et al.*, 2009; ten Cate and Okanoya, 2012). Arrangements of animal songs vary from 'simpler' songs (e.g. repetitions of one or two sound types in blue whales (*Balaenoptera musculus*) or fin whales (*B. physalus*) (McDonald *et al.*, 2006; Širović *et al.*, 2007) to the complicated patterns of certain birdsongs such as California thrashers (*Toxostoma redivivum*) or

Redthroats (*Pyrrholaemus brunneus*) (Taylor and Cody, 2015). Due to this variety, metrics of complexity are not universal (Edmonds, 1995). Repertoire size is often calculated by variables such as the total number of sounds produced, the number of unique sound types used (Neubauer, 1999; Boogert *et al.*, 2008; Templeton *et al.*, 2014), and/or song duration (Airey and DeVoogd, 2000; Zeng *et al.*, 2007). Higher-order estimates of information entropy can reflect complexity within sequential structure by measuring predictability (Shannon, 1948; Briefer *et al.*, 2010; Kershenbaum *et al.*, 2014a). How complexity is defined and measured should reflect the specific properties of the vocal display in question, particularly whether or not it contains higher-level structures.

Complexity measurements correlate with sexual selection in a number of oscine species (Nowicki *et al.*, 1998; Woodgate *et al.*, 2012; Suzuki *et al.*, 2014). Female songbirds such as zebra finches (*Taeniopygia guttata*) and European starlings (*Sturnus vulgaris*) prefer males with more complex songs (i.e. longer duration and containing a wider variety of sound types) (Searcy, 1992; Mountjoy and Lemon, 1996; Spencer *et al.*, 2005). This preference often occurs because song complexity can indicate male quality and fitness. It has been positively correlated with physical body condition (Catchpole, 1996; Lampe and Espmark, 2003; Kipper *et al.*, 2006; Pfaff *et al.*, 2007), ability to withstand physiological stress (Nowicki *et al.*, 2002), and neural structure (DeVoogd, 2004; Zeng *et al.*, 2007). Increased song complexity may also indicate an increased learning capacity. For example, it positively correlates with early neural development in great reed warblers (*Acrocephalus arundinaceus*) which underpins song learning (Nowicki *et al.*, 2000), and the uptake of novel tasks, as seen in zebra finches (Boogert *et al.*, 2008). Known as the 'cognitive capacity hypothesis' (Boogert *et al.*, 2008; Templeton *et al.*, 2014), this suggests that highly complex songs require more developed abilities in the acquisition, interpretation, and use of information (Catchpole, 1996).

Male humpback whales (*Megaptera novaeangliae*) produce a complex vocal display that is culturally learned and transmitted (Payne and McVay, 1971; Noad *et al.*, 2000; Garland, 2011). Speculations about the song's function focus on inter-sexual selection like that seen in bird songs (Payne and McVay, 1971; Tyack, 1981; Payne *et al.*, 1983; Smith *et al.*, 2008), though an intra-sexual function in males is also possible (Winn and Winn, 1978; Darling and Bérubé, 2001; Darling *et al.*, 2006; Dunlop and Noad, 2016). Songs are arranged in a nested hierarchy and are sung in a stereotyped pattern (Payne and McVay, 1971; Cholewiak *et al.*, 2013). Single sounds or 'units' are arranged in a sequence called a 'phrase'. Phrases are repeated multiple times to create a 'theme'. Four to seven different themes are sung in a consistent order, creating a 'song' (Payne and McVay,

1971). Despite all males in a given population conforming to the same song (Payne and Payne, 1985), the song itself constantly changes (Payne *et al.*, 1983). Songs that progressively change for one or two years are known as 'evolutions'. Evolutions can involve small changes to the entire song or modification of certain themes ('evolving themes') while other themes are replaced. In Australia, songs from the western population of humpback whales may enter the eastern population which is normally separate. The new songs are taken up by the eastern population, resulting in a sudden change to the entire song and all its themes, known as a 'revolution' (Noad *et al.*, 2000; Rekdahl, 2012b). Garland et al. (2011) showed that, whether evolutionary or revolutionary, songs move from eastern Australia further eastwards across the South Pacific, through a number of other humpback whale populations. This horizontal cultural transmission demonstrates cultural exchange on a spatial and temporal magnitude thus far documented only in humans (Garland *et al.*, 2011).

Understanding how song complexity changes over time can help to determine any potential relationships with learning or its possible function. Song complexity measures developed for birdsong have not been applied to quantifying complexity in humpback whale song, nor have potential changes in complexity been explored over the timescale presented here. The current study quantified song complexity in the east Australian population over 13 consecutive years, with complexity defined here by both repertoire size and structural traits such as unit arrangement or repetition. Revolutions introduce substantial amounts of novel material and cognitive constraints may limit the learning of the new song. We hypothesize that such a constraint would result in songs with lower complexity occurring immediately after song revolutions. It is also hypothesized that complexity will increase as songs evolve because there is more time to learn novelties and changes that can be progressively added to an existing song. Quantifying complexity in humpback whale song will inform the understanding of social learning capacity in humpback whales and other vocal learning species.

3.3 Methods

3.3.1 Data collection

Recordings of humpback whale song were made every year from 2002-2014. Study sites were located along the migratory corridor for east Australian humpback whales on the coast of southeast Queensland, Australia (Paterson and Paterson, 1984). Data were collected at two main locations: Peregian Beach (26°30' S, 153°05' E), Sunshine Coast, and Point Lookout (27°43' S, 153°53' E) North Stradbroke Island.

At Peregian, most recordings were collected using five-buoy moored hydrophone array deployed 1.5-2.5 km off the coast in the austral spring of 2002-2004, 2008-2011, and 2014. Buoys were placed approximately 750 m apart in water ranging in depth from 18-28 m. An onshore base station received VHF radio signals from the buoys using a four-channel receiver (type 8101 Sonobuoy) for buoys 1-4 and a single channel FM downconverter connected to a commercial FM hi-fi receiver for buoy 5. Signals were digitised and stored as 10 minute WAV files using *Ishmael* acoustic software (Mellinger, 2001) at a 22 kHz sampling rate and a 16 bit depth.

Array recordings were complemented by boat-based recordings of singing whales using Cleavite CH17, GEC Marconi SH101X, or High Tech Inc. HTI-96-MIN hydrophones (frequency response 30 Hz-20 kHz ±3dB) and Sony DAT, Microtrack, or Zoom digital recorders (WAV files with 44.1 kHz sampling rate and 16-bit depth). Boat-based recordings supplemented data collection in all years, but were the sole source of recordings from 2005-2007. Autonomous recorders (Acousonde 3A with external battery housings, Greenridge Sciences) were also used from 2012-2014. Two were deployed off the coast of Peregian Beach, each with a sampling rate of 25,818 Hz, a 9kHz low pass filter, and 20 dB gain. Recorders were placed side by side approximately 1.5 km from shore. Each Acousonde had a 12-hour duty cycle, one recording from 00:00 to 12:00 and the other from 12:00 to 00:00, to allow for continuous recording.

3.3.2 Song selection and transcription

Spectrograms of all recordings were generated using Raven Pro 1.4 (www.birds.cornell.edu/raven) for visual and aural inspection, with a Fast Fourier Transform (FFT) of 2048, Hann window, and 90% overlap. Recordings suitable for analysis had a signal-to-noise ratio (SNR) of at least 10 dB above the background noise. A dictionary of unit types for this dataset was created in Chapter 2 (Allen *et al.*, 2017) based on a subset of units classified by a self-organising map (SOM) (Allen *et al.*, 2017). Each unit type was assigned a number. In the current study, songs were transcribed by a human classifier (JA) into a numeric sequence of units, using this dictionary as a guide. Thirty-six transcribed song cycles were analysed from each year, excepting 2006 (12 cycles) and 2007 (4 cycles) due to a lack of recordings in those years. A full series of successive themes without repetitions of any singular theme was designated as a complete song cycle (Payne and Payne, 1985). No more than six cycles came from any individual singer. Song cycles were considered to be from a single individual if they were recorded in succession with no break in singing and the received level (i.e. loudness) was constant or changed slowly. Songs from separate recordings were assumed to be separate individuals. Because these recordings were

made during migration, it was assumed that singers on separated days had not been previously recorded (Noad and Cato, 2007; Horton *et al.*, 2011; Kavanagh *et al.*, 2017). This resulted in a total of 412 complete song cycles from 95 singers over the 13 consecutive years (see Table 3.1).

Table 3.1 Sample size of singers and song cycles used in each year.

Year	Singers	Song Cycles	Year	Singers	Song Cycles
2002	6	36	2009	6	36
2003	7	36	2010	8	36
2004	8	36	2011	9	36
2005	7	36	2012	13	36
2006	2	12	2013	9	36
2007	1	4	2014	10	36
2008	9	36			

3.3.3 Quantitative verification of themes

Following the methods of Chapter 2, qualitatively identified themes were quantitatively verified using a Levenshtein similarity analysis, a methodology to compare sequences (Garland *et al.*, 2012; Murray *et al.*, 2018). This analysis was weighted to account for quantified similarity in the acoustic features of some units (Allen *et al.*, 2017; Garland *et al.*, 2017b). Acoustic similarity of units was quantified based on the spatial layout of the acoustic dictionary used for transcription (for details, see Chapter 2). LSI was calculated between every possible pair of phrase repetitions in a given year and hierarchically clustered to ensure that qualitative theme assignments were robust (see Chapter 2). Resulting dendrograms from each year (2002-2014) showed that identified themes or theme variants clustered separately onto major branches (see Appendix 1). The cophenetic correlation coefficient (CCC) assessed how well the dendrograms represented associations within the data. Good representation requires a CCC score of 0.8 or higher (Sokal and Rohlf, 1962). CCC scores for the current study were greater than 0.85 for all years. Dendrograms from every year with labels for every theme are in Appendix 1.

3.3.4 Quantitative verification of evolutions and revolutions

LSI was also implemented to classify each year's song as either an evolution (i.e. it progressively evolved from the previous year) or a revolution (i.e. a complete replacement occurred from the previous year) based on the themes making up each song. For each year, LSI determined the similarity between every phrase repetition representing a theme. The phrase repetition with the highest similarity to all other phrases of a given theme was known as that theme's 'set median'

(Kohonen, 1985). Set median phrases were generated for every identified theme in every year. LSI values were calculated between every pair of theme set medians in adjacent years. If a pair of themes had greater than 20% similarity then they were defined as 'evolving', meaning that the same general theme occurred in both years but with a modified unit sequence in the latter year. Themes with 0% similarity between them were substantially different enough unrelated to be considered unrelated. Evolving songs contained several related or 'evolving' themes, while revolution events occurred when all themes had 0% similarity with the themes in the previous year's song.

The resulting LSI matrix of theme similarities was used as a cost matrix to identify songs as either evolutions or revolutions compared to the previous year's song. Set medians were also generated for each year's song based on its sequence of themes (e.g. a song's set median could be [A B C], meaning that the song's pattern was theme A, followed by theme B, followed by theme C). The cost matrix of theme similarities allowed a separate LSI between song types to be weighted based on whether or not they contained related themes (Rekdahl, 2012b). Unrelated themes were assigned a maximum weighting of cost=1, while substitutions of related themes were assigned a weighting cost proportional to their respective LSI values (Garland *et al.*, 2012; Garland *et al.*, 2015). Song changes were classified as an evolution if its similarity to the previous year's song was greater than 20%, indicating sufficient retention of the theme's pattern from one year to the next. This indicated that versions of the same themes (although modified) were present in the song pattern of both years. Revolutions were songs which contained 0% similarity between itself and the preceding song, indicating no shared themes due to a complete replacement of the song's pattern (Rekdahl, 2012b).

3.3.5 Complexity scores

To measure complexity within a song's structure and arrangement, a 'complexity score' was generated for each year's song following the methods of Boogert *et al.* (2008) and Templeton *et al.* (2014). While the measure was developed to analyse the songs of zebra finches (*Taeniopygia guttata*), we adapted it here to include variables (listed below) deemed the most relevant and informative for the structural properties of humpback whale song. The complexity scores were calculated at two levels within the song: the *song* level represented the full sequence of units (i.e. the complexity of the entire song irrespective of themes), and the *theme* level represented complexity with respect to the presence of themes. Individual theme-level complexity was calculated for every theme in each year's song, and the mean for all themes in each song was included as a variable in the complexity scores for the song as a whole. Three complexity scores

were generated: one using the song level variables, one using the theme level variables, and a total score which combines all variables from both level.

For the current study, six variables were used which represent complexity at multiple levels within the hierarchical structure of the song. Each variable was calculated for each song cycle transcribed (36 cycles for each year except 12 in 2006 and 4 in 2007).

Variables for 'song level' complexity

1. Number of units per song cycle
2. Number of unit types per song cycle
3. Duration of each complete song cycle in minutes

Variables for 'theme level' complexity

4. Number of themes per song cycle
5. Mean phrase duration per song cycle in seconds
6. Mean individual theme complexity score per song cycle, an average of complexity scores calculated for each separate theme from the following variables derived from all of a theme's phrase repetitions:
    a. Number of units per phrase repetition
    b. Number of unique unit types per phrase repetition
    c. Duration of each phrase repetition in seconds

The total number of sounds, the number of unique sound types, and song duration are variables previously used to assess song complexity in both birds and mammals (Boogert *et al.*, 2008; Cholewiak *et al.*, 2013; Templeton *et al.*, 2014; Murray, 2015). The theme-level measurements were included to capture the additional complexity of humpback songs' hierarchical arrangement.

All statistical tests were run using *R* (Version 3.3.0, R Core Development Team, 2016). All six variables were first natural log-transformed to ensure a normalized distribution based on the Kolmogorov-Smirnov test of normality. Correlation between variables, determined by Pearson correlation coefficients, indicated that all variables had similar relationships with the data (See Results, Table 3.2). This allows them to be condensed using a principal component analysis (PCA) and represented by a single composite score. When variables are uncorrelated and result in multiple clusters, PCAs can simplify their structure by rotating axes to bring them in line with at least one

cluster of variables (Thurstone, 1947). In the current analysis, all variables were correlated and so an unrotated PCA was used. The first principal component score of the PCA provides a composite of all the input variables, which served as the complexity score. Each score directly associates with complexity, such that higher scores indicated higher complexity levels. Scores were dimensionless and had no scale or units, but were comparable amongst each other because principal components use multidimensional scaling to combine variables with different units. The slope of the linear trendline between adjacent complexity scores represented the rate of change in song complexity over time.

Individual theme complexity scores (theme-level variable #6, as calculated following the method described above) were also separately compared between sets of highly similar evolving themes (i.e. themes that occurred in multiple years with at least 20% similarity based on LSI anlaysis) to quantify how complexity changed within themes as they were modified from year to year. Themes which only appeared in a single year could not be compared in multiple years and were excluded from the comparative analysis of individual themes. Comparison of individual theme scores was necessary to provide a detailed understanding of exactly how complexity changed at the theme level for the specific themes that evolved over multiple years.

3.3.6 Information entropy estimates

Entropy quantifies how predictably a sequence is arranged (Shannon, 1948). Second-order entropy estimates calculate this predictability in terms of the conditional probabilities between any two units in the song. Conditional probabilities are the probability of one unit following another in a sequence (Shannon, 1948). Second-order entropy estimates were calculated using the following equation:

$$H_2 = -\sum_{i,j}^{N} P(i)P_i(j)\log_2 P_i(j)$$

where H_2 is second order entropy, *P(i)* is the probability of occurrence of element *i*, *Pi(j*) is the probability of occurrence of unit *j* given the preceding unit is element *i*, and *N* is the number of elements (types of units) in the repertoire (Shannon, 1948). Entropy estimates for each year were calculated separately for 1) sequences of themes (i.e. the pattern of different themes making up a song, omitting the units that make up those themes) and 2) sequences of units (i.e. the pattern of units making up the entire song). Separate estimates account for the multiple hierarchical levels of the song's structure.

3.3.7 Phrase variants

All unit sequences of phrase repetitions were evaluated through a separate cluster analysis based on LSI values. Every major dendrogram branch represented a theme or theme variant (see Appendix 1). Within those major branches, each individual terminal branch represented a 'phrase variant' of that particular theme (i.e. multiple arrangements of the same theme). Unique variants were sung by a single individual, while shared variants were sung by at least two singers (Murray, 2015). It should be noted that phrase variants are not necessarily substantially different to one another. For example, if a theme's general pattern is AABBCC then two different phrase variants might be 1) AABBBCC and 2) AAABBCCC. Variant #1 might be sung by multiple individuals (i.e., 'shared') while variant #2 might only be sung by a single individual (i.e., 'unique'). These small differences in separate variants allow them to maintain a high degree of similarity to one another. Years with less than six singers were excluded to ensure a representative sample size (Garland, 2011). Therefore, 2006 (two singers) and 2007 (one singer), were excluded. The number of different phrase variants recorded was tallied per year.

3.4 Results

3.4.1 Song complexity

Complexity scores served as a reliable indicator of changes in song complexity over time. The six variables of the total complexity score were all positively correlated (Table 3.2) and had loading coefficients ranging from 0.38 to 0.61 (Table 3.3). The unrotated PCA of all variables extracted a single principal component which explained 68% of the variance with an eigenvalue of 4.1. When the three song-level variables (number of units per song cycle, number of unit types per song cycle, duration of each song cycle) were use the PCA extracted a single principal component which explained 83% of the variance with an eigenvalue of 2.5. When the theme-level variables (number of themes per song cycle, mean phrase duration per song cycle, mean individual theme complexity score per song cycle) were used, the PCA extracted a single principal component which explained 81% of the variance with an eigenvalue of 2.4.

Table 3.2 Pearson correlation coefficients (r) for the six variables incorporated into the total complexity composite score.

Variables	Total units	Total unit types	Song duration (min)	Number of themes	Mean phrase duration (s)	Mean theme-level complexity
Total units	NA	r=0.74	r=0.69	r=0.63	r=0.63	r=0.80
Total unit types		NA	r=0.85	r=0.37	r=0.51	r=0.55
Song duration (min)			NA	r=0.51	r=0.45	r=0.37
Number of themes				NA	r=0.75	r=0.59
Mean phrase duration (s)					NA	r=0.80
Mean individual theme complexity						NA

Table 3.3 Principal component analysis (PCA) loading coefficients for the six variables used in the total complexity score, the three variables used in the theme-only score, and the three variables used in the song-only score. Loading coefficients are the coefficient of correlation between each variable and the principal component score which serves as the complexity score.

Variables	Loading Coeff. Total Complexity	Loading Coeff. Theme-Only	Loading Coeff. Song-Only
Total units	0.46	N/A	0.54
Total unit types	0.41	N/A	0.59
Song duration (min)	0.38	N/A	0.61
Number of themes	0.39	0.56	N/A
Mean phrase duration (s)	0.40	0.60	N/A
Mean individual theme complexity	0.40	0.57	N/A

Scores for each separate year were extracted, providing three sets of complexity scores. All complexity scores were highly correlated (Pearson correlation coefficient, $p<0.05$ for all) and formed a quasi-sinusoidal pattern over time (Fig. 3.1). They increased during evolutionary transitions and decreased with revolutionary transitions. This showed that after revolutions, songs contained fewer sounds and sound types, and had shorter overall song cycle duration. They also contained fewer themes, and those themes individually had shorter phrase repetitions and contained fewer sounds and sound types. A summary of these features in each year can be found in Table 3.4. Total complexity increased during evolutions at a mean rate of 2.9 per year (range = 1.9-4.9) and decreased at a mean rate of 2.6 per year (range= 0.9-5.6).

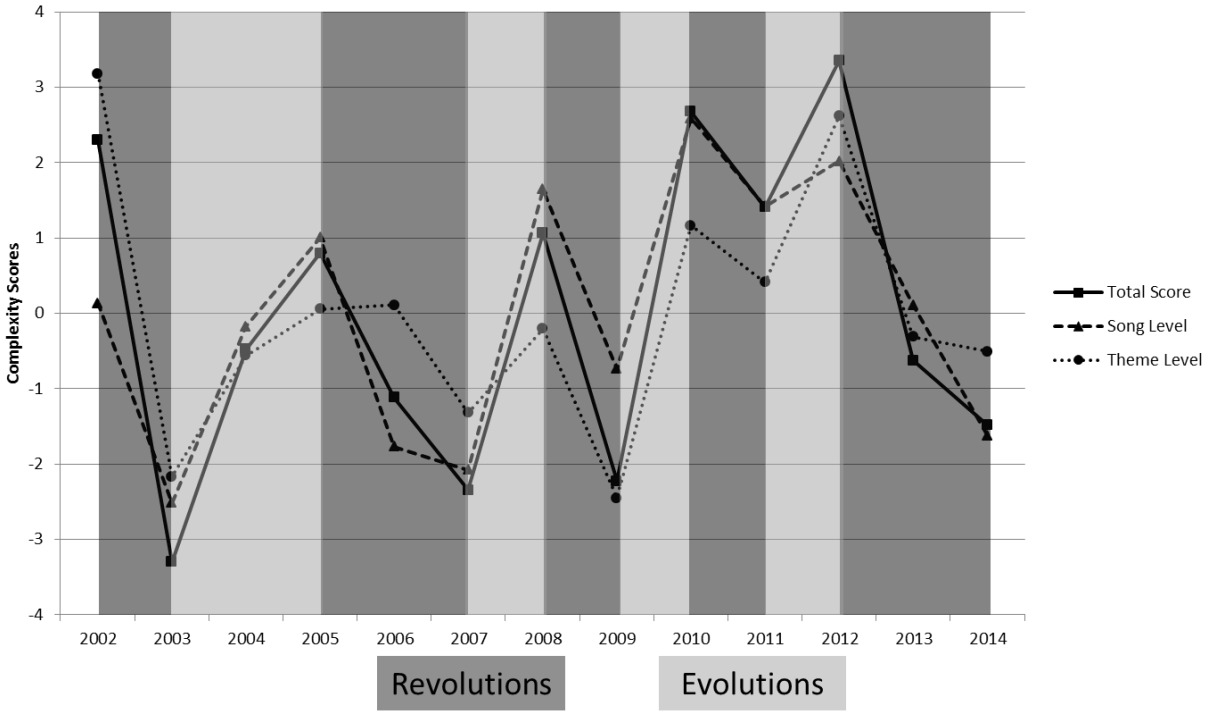

Figure 3.1 Song complexity scores for each year (2002-2014). Three scores were calculated using 1) song-level variables only (number of units, number of unit types, song cycle duration), 2) theme-level variables only (number of themes, mean phrase duration, mean theme complexity), and 3) all variables combined into a total score. Revolution and evolution transitions are demarcated. Changes in the rate of complexity were calculated from the slope of the trend lines in adjacent years

Table 3.4 Summary of variables used in the song complexity scores. The mean and range for each of the variables used in the composite song complexity score. Theme-level complexity had no units, as it was calculated through multi-dimensional scaling.

Year	units	unit types	song duration (min)	# themes	mean phrase duration (sec)	mean theme-level complexity score
2002	171	20	7.4	6.9	22.7	0.5
2003	101	11	5.2	3.8	13.0	-1.2
2004	153	19	7.7	4.4	14.6	-0.2
2005	215	22	7.6	4.0	16.3	0.3
2006	123	18	4.3	3.9	15.9	0.5
2007	113	16	4.3	3.5	14.8	-0.6
2008	218	24	9.0	5.3	15.5	-0.5
2009	160	15	7.0	2.8	13.1	-1.0
2010	228	25	11.1	4.7	19.3	0.4
2011	198	28	7.7	4.3	16.1	0.6
2012	197	30	9.0	6.5	19.5	0.9
2013	157	19	6.9	4.9	14.2	-0.4
2014	204	16	6.3	3.7	16.3	-0.1
Mean	172	20	7.2	4.5	16.3	-0.1
Range	[101-228]	[11-30]	[4.3-11.1]	[2.8-6.9]	[13.0-22.7]	[-1.2-0.9]

3.4.2 Complexity of evolving themes

The three variables (number of units, number of unit types, phrase duration) which generated the individual theme complexity scores all had strong positive correlations (Table 3.5). The first principal component score from the unrotated PCA extracted one principal component which explained 87% of the variance with an eigenvalue of 2.6.

Table 3.5 Pearson correlation coefficients (r) and loading coefficients for the three variables incorporated into the individual theme complexity composite score. These scores were also used to calculate mean individual theme complexity for the total complexity score.

Variables	Total units	Total unit types	phrase duration (s)	Loading Coefficient
Total units	**NA**	**r=0.81**	**r=0.78**	**0.58**
Total unit types		**NA**	**r=0.82**	**0.57**
Phrase duration (s)			**NA**	**0.58**

The individual complexity scores increased over time for all evolving themes with the exception of the two themes from 2011-2012 (Fig. 3.2). Evolution of themes therefore generally included increases in the number of units and/or unit types and a lengthening of phrase repetitions (Table 3.6). In years with increasing complexity, it changed at a mean rate of 0.7 per year (range= 0.1-1.7). It decreased at a mean rate of 0.2 per year (range= 0.1-0.3). Rate of change in individual theme complexity was significantly lower than rate of change in total complexity of entire song (heteroscedastic t-test, $p<0.01$). Changes occurring in individual themes (e.g. increases in the number or units) were therefore smaller or less drastic than the changes that occurred in the song as a whole.

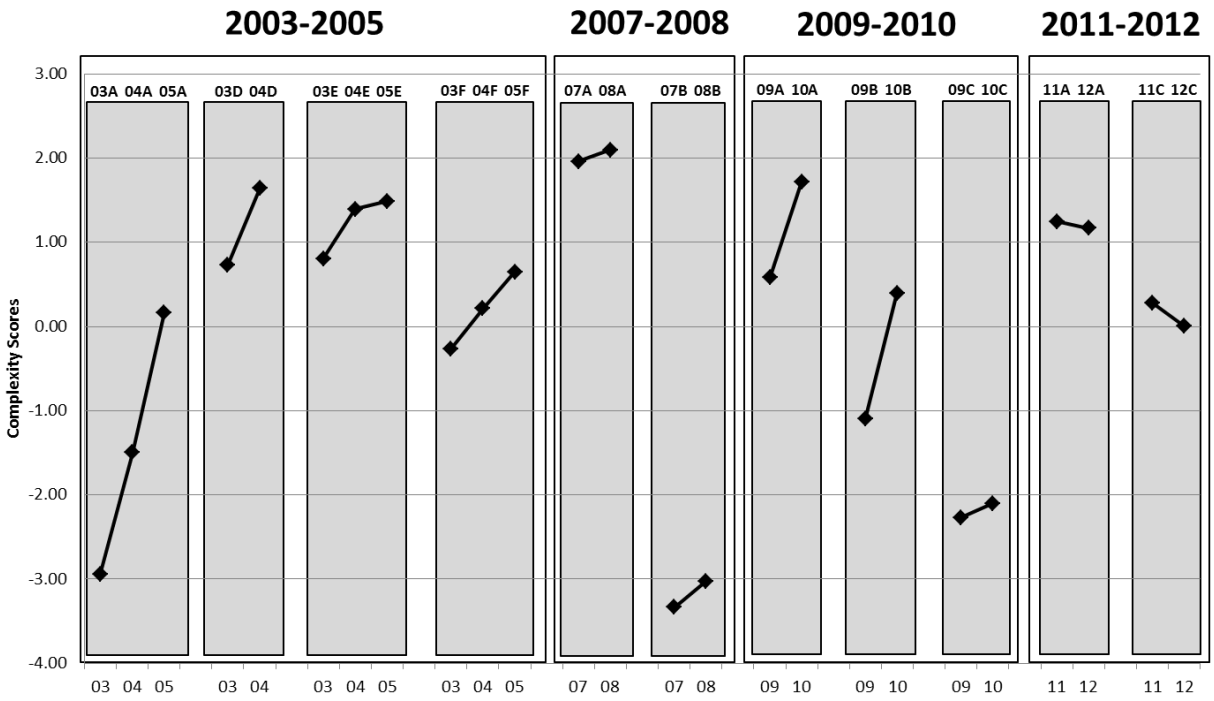

Figure 3.2 Individual theme complexity scores for evolving themes. Each theme's complexity scores over time are represented within its respective box. Boxes contain each set of evolutionary themes, meaning that the theme progressively evolves from one year to the next (as indicated by the years on the x-axis). Each theme was labelled with two numbers indicating the year (02-14) and a letter to differentiate it from the other themes in each respective year. For example, theme 03D occurred in 2003 and evolved into 04D, which occurred in 2004. All other themes occurred in a single year and are detailed in Appendix 1. The rate of change in complexity score is indicated by the slope of the trend lines in adjacent years. See Appendix 2 for spectrograms of evolving themes

Table 3.6 Summary of each variable used in the composite theme complexity score for evolving themes. Note that this table excludes all themes that only occur in a single year. A complete list of all themes is in Appendix 1. Spectrograms of all evolving themes listed here are in Appendix 2.

Theme	Year	Mean Units	Mean Unit Types	Duration
03A	2003	2.0	2.0	7.4
04A	2004	3.0	3.0	8.7
05A	2005	7.7	4.1	9.7
03D	2003	10.1	3.0	18.5
04D	2004	13.1	4.0	19.9
03E	2003	11.2	3.2	17.0
04E	2004	8.6	4.5	19.4
05E	2005	7.6	4.6	22.9
03F	2003	5.8	2.9	14.6
04F	2004	5.6	3.4	16.8
05F	2005	7.6	3.1	21.2
07A	2007	10.1	5.1	22.4
08A	2008	11.6	4.7	24.8
07B	2007	2.0	2.0	5.5
08B	2008	2.0	2.0	6.7
09A	2009	8.0	3.4	16.7
10A	2010	8.0	4.8	24.3
09B	2009	3.4	2.6	13.7
10B	2010	5.1	3.3	21.5
09C	2009	3.0	2.0	9.0
10C	2010	3.0	2.0	10.2
11A	2011	6.3	4.5	22.9
12A	2012	7.1	3.6	27.3
11C	2011	4.9	4.3	14.3
12C	2012	5.0	3.0	18.4
Mean		6.5	3.4	16.5
Range		[2.0-13.1]	[2.0-5.1]	[5.5-27.3]

3.4.3 Information entropy estimates

Second order entropy estimates of theme sequences ranged from 0.04 to 0.6 bits with an average of 0.3 bits (Fig. 3.3). Entropy estimates of unit sequences for entire song cycles ranged from 0.7-1.8 bits with an average of 1.2 bits. There were no consistent relationships between either entropy estimate and song transitions (revolutions or evolutions). Complexity had no correlation with entropy of either unit sequences (Pearson correlation coefficient, $p=0.52$) or theme sequences (Pearson correlation coefficient, $p=0.17$). Therefore, how predictably unit and theme sequences were arranged was unrelated to how complex the song was. Increases in features such as the

number of units in a song cycle or a song's duration did not result in the song's unit sequences becoming less predictable (i.e. higher entropy). Similarly, increases in theme-level features such as the number of themes present within a song cycle did not result in less predictable theme sequences.

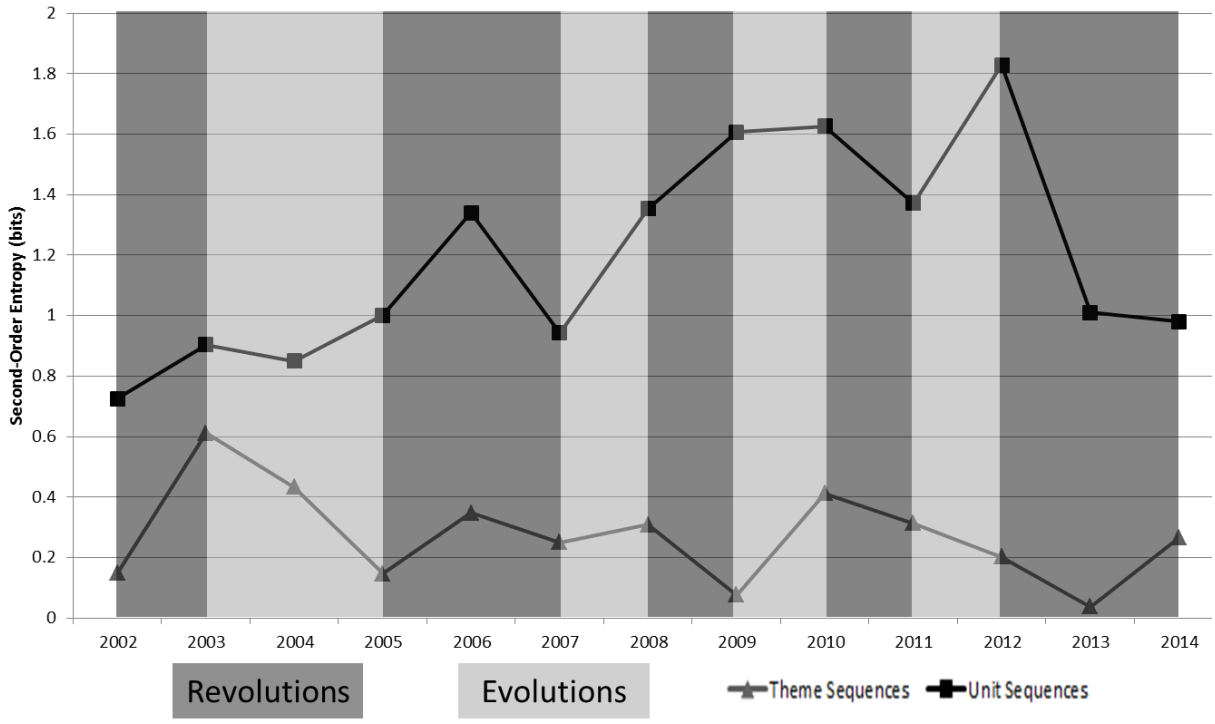

Figure 3.3 Second-order entropy estimates for theme sequences and unit sequences from 2002-2014 in relation to revolution and evolution transitions.

3.4.4 Phrase variants

The total number of recorded phrases in each year's dataset (based on all 412 song cycles) ranged from 703 to 1863 with a mean of 1158 (+/- 297). Of the phrases recorded each year, the proportions that were individually unique phrase variants (i.e. phrase types sung by a single individual) ranged from 12.3% to 60.5% with a mean of 34.3% (Fig. 4.4). The proportions of unique variants were correlated with entropy estimates of theme sequences (Pearson correlation coefficient, $p<0.05$) and all complexity scores (Pearson correlation coefficient, $p<0.05$ for all), but were not correlated with entropy estimates of unit sequences (Pearson correlation coefficient, $p=0.35$).

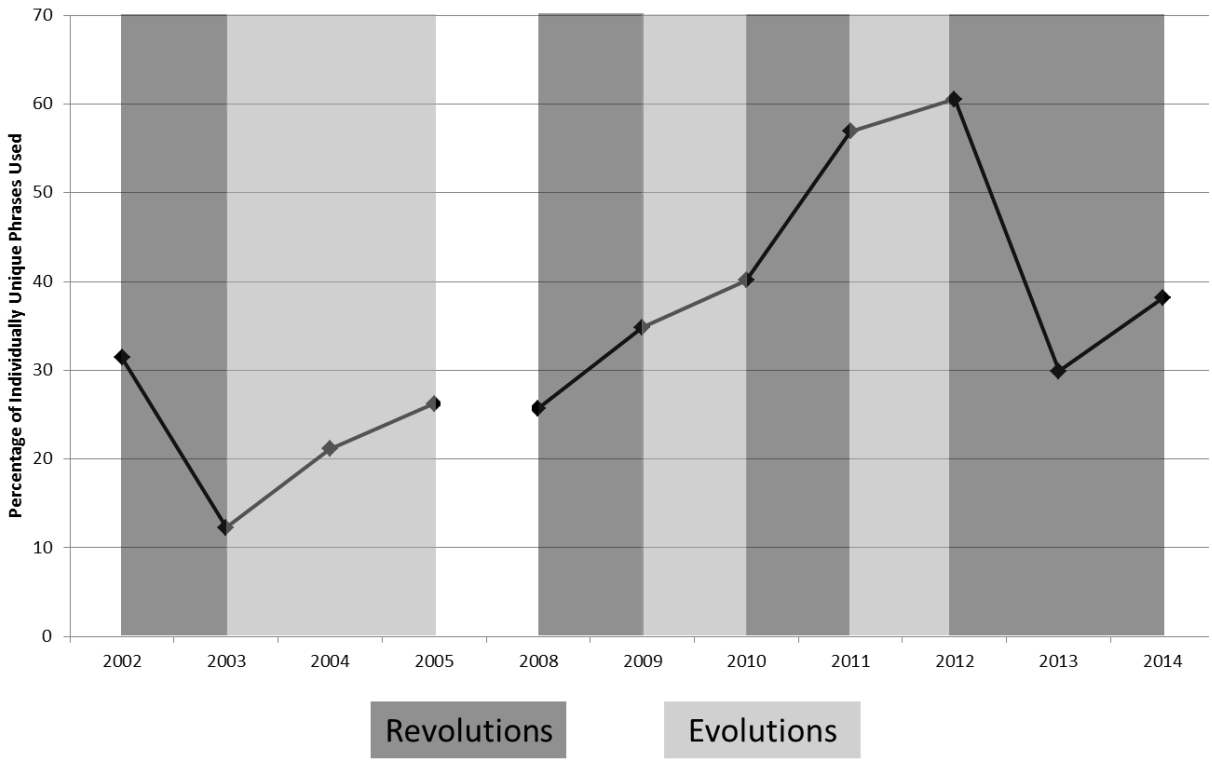

Figure 3.4 Proportion of individually unique phrase variants in each year. Phrase variants were designated as individually unique if the variant was only recorded from a single individual. Note that 2006 and 2007 are excluded due to small sample size

3.5 Discussion

Song complexity displayed a clear relationship with yearly song changes. Small and progressive changes made songs more complex as they evolved. When radical changes occurred during revolution events, the song was completely replaced with a simpler one. This relationship remained consistent for scores at both the song-level (total units, total unit types, total song duration) and theme-level (number of themes, mean phrase duration, mean theme complexity). Therefore, changes at both hierarchical levels of the song contribute to changes in its complexity (Table 3.4). Features of the song's entire display (the number of units, number of unit types, and length of the entire song display) and features of the song's themes (the number of themes, length of phrase repetitions, and average complexity of individual themes) all increased when the song evolved and decreased when a revolution occurred. Further supporting this is the parallel trend seen in evolving themes, whose complexity also increased over time with evolutionary changes (with the exception of 2011 and 2012). This trend held true for themes with both simple (low individual theme complexity) and complex (high individual theme complexity) arrangements, demonstrating that complexity within themes increases irrespective of their initial levels of complexity. There was no consistent rate at which complexity changed over time. However, evolving themes had

significantly lower rates of change than at the song level. Therefore, the changes that occur within each individual theme combine with broader changes such as the number of themes or duration of phrase repetitions to influence the overall complexity of the song as a whole.

Entropy is a poor gauge of general song complexity (Kershenbaum, 2014), but does quantify complexity in sequential structure (Kershenbaum *et al.*, 2014a). Although both measures account for number of unit types and themes, entropy includes a measure of predictability that the song complexity measure lacks. There was no relationship with either complexity or whether or not a song was an evolution or revolution. Entropy estimates quantifies the degree of predictability seen at both levels of the song's internal structure: units can be predicted based on the preceding unit, but not nearly as reliably as the ability to predict a theme based on the preceding theme. Results of previous studies using the Markov first-order model (equivalent to the methods used here) found similar unit-level estimates to those found here (Suzuki *et al.*, 2006; Miksis-Olds *et al.*, 2008). While such predictability is expected in a song display as stereotyped as humpback whale song, what was unexpected was that predictability at each level remains relatively consistent over time despite changes to song complexity or arrangement (Briefer *et al.*, 2010). Such predictability in the song's fine-scale arrangements is likely to make songs easier to learn and remember, even when the song has a complex pattern (Guinee and Payne, 1988; Handel *et al.*, 2012).

Previous studies have suggested that complexity in humpback whale song structure and its evolutionary nature present a well-developed memory capacity (Guinee and Payne, 1988; Parsons *et al.*, 2008; Handel *et al.*, 2012). The changing nature of song complexity identified here supports this. Evolutions may suggest an ability to remember song arrangements and their progressive changes over both the short term (several weeks or months) and long term (multiple years). However, the short span of evolutions (2-3 years) and subsequent decline in complexity during revolution events may indicate a possible constraint on long term memory of song patterns beyond a few years of progressive changes.

Progressive changes to the song's arrangement are thought to come from the novel material each singer adds to his own song (Noad *et al.*, 2000; Arraut and Vielliard, 2004; Garland *et al.*, 2011; Cholewiak *et al.*, 2013). Parallel increases in complexity and individuality during evolutions, in combination with the consistently predictable arrangements may indicate that increased complexity represents embellishments to the song rather than additional information content. Singers may be attempting to make their own songs more complex in an effort to stand out

amidst the population's persistent conformity. This would follow the 'anti-habituation hypothesis', which suggests that bird song contains variation to avoid individuals becoming so used to a song that it can no longer serve its function (Krebs, 1977). Correlation of individuality with theme sequence entropy may suggest that more unique songs use more themes, thus creating less predictability in the theme sequences. However, statistical correlation does not always indicate biological meaning. In particular, the missing data points (2006 and 2007) from individuality prevent definitive comparisons with either complexity or entropy. Confounding variables such as the consistent increase in population size over the study period (Noad *et al.*, 2011; Noad *et al.*, 2017) could influence both individuality and entropy. More information on population size and individual singers will better clarify the relationship between individuality and either complexity or entropy.

Similarity analyses between western and eastern Australian song show that revolutionary transitions in eastern Australia originate in western Australia (Rekdahl, 2012b). The new songs are introduced into the eastern Australian population with a one or two year delay (Rekdahl, 2012b). Revolutions, by definition, contain large amounts of novel material. This degree of novelty is likely to greatly exceed the small amounts of novel material normally added to evolving songs each year. If the inclusion of novelty in an established song type promotes an individual's fitness, perhaps it is more advantageous to learn a new, completely novel (albeit simpler) song than to add complexity to the current song (Noad, 2002). Revolutions occur every two to three years (Garland *et al.*, 2011; Rekdahl, 2012b), so complexity in this population appears to have a limited period of growth before being 'reset' by a new song. Many species have similar constraints on their capacity to learn increasingly complex vocal displays for a variety of reasons (Petkov and Jarvis, 2012). Despite its complexity, humpback whale song does not require a high energetic cost (Helweg *et al.*, 1992). Song complexity may be indicating learning ability as a possible fitness metric (as theorized by the cognitive capacity hypothesis) rather than physical quality (Noad, 2002; Templeton *et al.*, 2014).

It is currently unclear whether revolutions and the accompanying changes in complexity are driven by constraints to opportunity or ability. The uptake of the new song could be driven by the need for a simpler song once the current one has reached an upper limit of complexity. Alternatively, cultural revolution events require singers to learn a lot of novel material at once rather than incrementally as with small evolutionary changes. A way to explore these hypotheses would be to determine complexity for the west Australian song types that are transferred to east Australia. If equivalent songs have equivalent complexity, the east Australian population may pick

up the west Australian song because their own has begun to reach their learning threshold and the new song is simpler. If equivalent songs have higher complexity in west Australia, then east Australian whales may adopt a simplified version of western Australian's song. This would imply that constraints impact the ability of singers to learn the large amounts of novel material presented during revolution events rather than their ability to learn increasingly complex arrangements.

Any potential learning constraints identified here may differ from those present in other populations, as cultural revolutions thus far appear to be a phenomenon unique to the South Pacific. The complexity measurements developed here should be applied to a population from another ocean basin, such as Hawaii, to determine how complexity changes without revolution events. I hypothesise that complexity would still fluctuate in a similar oscillating pattern due to cognitive limitations on learning. However, since novel material is introduced at a more gradual and consistent rate due to constant evolutions, I hypothesise that these fluctuations in complexity would occur over a longer period and in smaller amounts. In other words, complexity might increase gradually over several years, then decrease to a marginally simpler song. Quantifying the complexity patterns in a constantly evolving song would determine how cultural revolutions influence song learning and clarify what learning constraints might be present across populations.

The complexity of vocal displays provides important insight into the structure, learning mechanisms, and evolution of animal communication and vocal displays (Kershenbaum *et al.*, 2014a; Patricelli and Hebets, 2016). Although it has been studied to varying degrees in a number of species (Boogert *et al.*, 2008; Stephan and Zuberbühler, 2008; Bohn *et al.*, 2009; Briefer *et al.*, 2010; Kershenbaum *et al.*, 2012), research on complexity measures and trends in humpback whale song have been limited (Cerchio *et al.*, 2001; Suzuki *et al.*, 2006; Smith *et al.*, 2008; Green *et al.*, 2011; Murray *et al.*, 2018). While it serves as an indirect method for studying social learning, the song remains a striking example of a culturally transmitted display in animals. Changes in complexity over time can help clarify influential factors in the processes of song learning and transmission, such as the possible constraints on social learning capacity identified here. This will lead to a more comprehensive grasp of cultural learning in non-human species. More knowledge about cultural learning in animals can help us to better understand its evolution and the current role it plays in humans.

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CHAPTER 4 Network analysis reveals underlying syntactic features in a mammalian vocal learning display, humpback whale song

4.1 Abstract

The arrangement of acoustic signals into vocal displays is typically governed by a set of syntactic rules. However, there is a limited understanding of which syntactic rules might be shared by the complex arrangements of vocal displays in different taxa. Recent work, focused on the complex repertoires and syntax of songbirds, has taken a new approach to investigating syntax. Network-based modelling quantifies song features such as the connectivity between signals (adjacent signals in a sequence) and other patterns in their arrangements. These features indicate structural complexity and are often the basis of syntax. Here, we apply network-based modelling to the complex, hierarchically structured songs of the humpback whale (*Megaptera novaeangliae*) over 13 consecutive years of song recorded from the east Australian population, to quantify the network structure and syntactic rules present. Given the song's evolving pattern each year and the cultural conformity of males in a population to learning that pattern, network modelling was applied to capture the patterns of multiple song types. In every year, song arrangements displayed "small-world" network structure characterised by clusters of highly connected sounds (units). The transitions between these connected units were further characterised by a combination of patterns indicative of structural stability and patterns indicative of structural variability. The presence of small-world network structure within the song's structure may facilitate the vocal learning observed. Similar small-world structures and transition patterns are also found in the song displays of several oscine species, indicating that syntactic patterns may be common among the complex vocal learning of multiple taxa. Understanding the syntactic rules governing the arrangement and structure of vocalisations in multiple, independently evolving lineages will indicate what rules may be important to the evolution of complex communication, including human language.

4.2 Introduction

Vocal communication systems have a set of rules that govern the arrangement of acoustic signals, broadly defined as 'syntax' (Marler, 1977; Berwick *et al.*, 2011; Kershenbaum *et al.*, 2014a). Most animal communications are characterised by 'regular' grammars (Kershenbaum *et al.*, 2014a), represented by some of the simplest arrangement rules (Chomsky, 1957). Examples of species which use regular grammar in their vocal sequences include primates (e.g., titi monkeys [*Callicebus moloch*], Robinson 1979; vervet monkeys [*Cercopithecus aethiops*], Seyfarth *et al.*, 1980; wedge-capped capuchin monkeys [*Cebus olivaceus*], Robinson 1984; Diana monkeys, [*Cercopithecus diana*], Zuberbühler 2002; wild gibbons, Clarke *et al.*, 2006), cetaceans (e.g., killer whales [*Orcinus orca*], Shapiro *et al.*, 2011; bottlenose dolphins [*Tursiops truncatus*], Janik 2009), free-tailed bats [*Tadarida brasiliensis*] (Bohn *et al.*, 2009), and the rock hyrax [*Procavia capensis*] (Kershenbaum *et al.*, 2012). A more complex set of rules are 'context-free' grammars, considered to be unique to human language (Hauser *et al.*, 2002; Fitch *et al.*, 2005). Context-free grammars allow for 'recursive' patterns in which meaningful sequences are embedded within one another (van Heijningen *et al.*, 2009). There is limited (though debated) evidence of context-free grammar in the songs of some bird species like the European starling (*Sturnus vulgaris*) (Gentner *et al.*, 2006), the skylark (*Alauda arvensis*) (Briefer *et al.*, 2010), and the zebra finch (*Taeniopygia guttata*) (van Heijningen *et al.*, 2009). As a result, the presence of complex syntactic rules remains contentious in non-human vocal displays.

Non-human vocal syntax has been extensively explored in birdsong. Birdsong can serve as a model for syntactic structure in animals due to similarities with human speech acquisition such as a latent learning period early in life, neural development, and imitation through exposure (Doupe and Kuhl, 1999; Bolhuis *et al.*, 2010; Berwick *et al.*, 2011). However, comparatively little is known about syntactic rules in mammalian species. Mammalian vocalizations likely share a closer evolutionary lineage to our own (Kershenbaum *et al.*, 2012). Humpback whale (*Megaptera novaeangliae*) song is a well-known and complex mammalian vocal display that provides a model to help understand more about the evolution of complex vocal communication. Their song repertoire is large and versatile, analogous to the more complicated birdsong displays. However, unlike birds, humpback whales produce songs in a stereotyped, nested hierarchy (Payne and McVay, 1971; Catchpole and Slater, 2008). Male humpback whales arrange individual sounds or 'units' in a stereotyped pattern to make up a 'phrase'. These phrases then repeat multiple times to form a 'theme'. A complete sequence of themes sung in a particular order comprises a 'song'. All male humpback whales in a population usually conform to the same song at any given time.

However, the song undergoes progressive changes, known as 'evolutions', each year which all singers adopt through social learning (Payne *et al.*, 1983; Rendell and Whitehead, 2001; Garland *et al.*, 2011). While songs become fixed in many oscine bird species, some evolve their songs through vocal learning and imitation similar to humpback whales (Nottebohm, 1970; Kroodsma, 2004). Understanding the structure, learning mechanisms and information content of humpback whale song may provide insight into how complex grammars and vocal learning evolve in a mammalian species (Janik and Slater, 2000; Kershenbaum *et al.*, 2012).

Traditionally, research on syntactic rules in vocal displays has focused on the complexities in repertoires, such as the number of elements (e.g., words in human language, syllables or phrases in birdsong, or sound units in humpback whale song) present or how often those sounds appear (Catchpole and Slater, 2003; Clarke *et al.*, 2006; Kershenbaum *et al.*, 2012). More recent studies have begun to include structural complexities such as connectivity between sounds (i.e. which ones appear together in a sequence) or transitions between connected sounds (Sasahara *et al.*, 2012; Deslandes *et al.*, 2014; Weiss *et al.*, 2014; Taylor and Cody, 2015; Cody *et al.*, 2016; Hedley, 2016). Network modelling has emerged as a tool for investigating these structural complexities. Some networks are randomly structured, which are defined by two features: their connections have no order, resulting in very little clustering (groups of highly connected points) and few steps connect points in the network (Rapoport, 1957). Networks can also be regular with all points equally connected (Watts and Strogatz, 1998; Newman, 2003). Regular networks have lots of clustering, but points in separate clusters can require many steps to connect them (Newman, 2003). 'Small-world' networks fall between these two extremes, with certain points being more connected than others (Watts and Strogatz, 1998). An analogous concept is known as 'six degrees of separation', where any two people in the world are separated by six points of connection (through acquaintances) (Guare, 1990; Watts and Strogatz, 1998). This illustrates the construct of a small-world network: high connectivity indicates that any two points within a network can be linked within a few steps. Small-world network structures can spread information quickly and efficiently through the network (Bullmore and Sporns, 2009), making them widespread among many complex systems. For example, urban street planning (Jiang and Claramunt, 2004), cortical hubs in the human brain (Achard *et al.*, 2006) and vocally learned systems like human language (Cancho and Solé, 2001) all display small-world network structures. Recent work shows that small-world networks are also common in complex birdsong repertoires such as those of the nightingale (*Luscinia megarhynchos*) (Weiss *et al.*, 2014), the California thrasher (*Toxostoma redivivum*)

(Sasahara *et al.*, 2012; Cody *et al.*, 2016), the house wren (*Troglodytes musculus*) (Deslandes *et al.*, 2014), and Cassin's vireo (*Vireo cassinii*) (Hedley, 2016).

Transition 'motifs' indicate local structural properties in the network by describing the arrangement of elements (e.g., reoccurring patterns of elements within the network) (Milo *et al.*, 2002). These transitions are categorised as either 'deterministic' or 'non-deterministic' motifs (Sasahara *et al.*, 2012). Deterministic motifs occur when only a few specific elements follow a particular element, while units in non-deterministic arrangements may be followed by a wide variety of elements (Sasahara *et al.*, 2012; Taylor and Cody, 2015). Typically, deterministic motifs occur in stereotyped displays, while non-deterministic motifs are found in either randomised or highly versatile displays (Sasahara *et al.*, 2012).

Another important structural feature is the frequency with which each element occurs within the display ('usage'). Usage can be modelled for its adherence to Zipf's law as a measure of repertoire complexity (McCowan *et al.*, 1999) and openness, defined as the amount of either redundancy (a 'closed' display with a few particular elements that are commonly used) or diversity (an 'open' display with more variety in which elements are used and how often units are used) in the repertoire (Briefer *et al.*, 2010). Zipf's law stipulates that word usage in human language has an inverse relationship with the rank of each word's use (Zipf, 1949; 1968). The second most commonly used word is used approximately half as much as the most commonly used word, the third most commonly used word is used approximately one third as much as the most commonly used word, etc. When the logarithm of rank is plotted against the logarithm of usage, there is a linear regression of approximately -1 for all human languages (Ferrer i Cancho and Solé, 2003). Known as a Zipf curve, this relationship occurs when there are a few common words while most words are relatively rare (Zipf, 1949). However, element usage of animal repertoires often have a convex departure from this linearity, known as a Mandelbrot fit to the Zipf curve, which typically has a slope of less than -1 and indicates more redundancy in unit usage (Mandelbrot, 1961; Hailman *et al.*, 1985; Briefer *et al.*, 2010). Examples of repertoires with a Zipf-Mandelbrot curve include the calls of chick-a-dees (*Parus atricapillus*) (Hailman *et al.*, 1985) and sagebrush lizards (*Sceloporus graciosus*) (Martins, 1994), as well as the songs of several birds including skylarks (Briefer *et al.*, 2010) and California thrashers (Cody *et al.*, 2016). Investigating how closely a species' element usage follows Zipf's law is useful as a baseline metric for estimating that system's potential for syntactic complexity (McCowan *et al.*, 2005; Koplenig, 2015).

Repertoire complexity has been quantified in humpback whale song (Chapter 3), but its structural complexity and syntactic rules have not. In the current study, recordings of the east Australian humpback whale song were assessed over 13 consecutive years. Three specific structural features of songs were measured each year using network modelling methods: 1) the overall network structure, 2) the distribution of unit usage (Zipf's law), and 3) transitions patterns. It is hypothesized that humpback whale song, given its complex structure, will contain both small-world network structure and a Zipf-Mandelbrot curve distribution as these features are common among complex and learned vocal displays. Firstly, each of the three structural features was assessed separately in each year. Secondly, each feature was combined across all years to quantify consistent syntactic patterns across all of the songs (Sasahara *et al.*, 2012). It is still unclear what syntactic rules are unique to certain displays and what are shared between complex communication displays of different species (Pinker and Jackendoff, 2005). Commonalities among syntactic rules in a mammalian vocal learning display will help to identify common vocal learning strategies or evolutionary roots across multiple taxa (Moore *et al.*, 2016).

4.3 Methods

4.3.1 Data collection

Data were collected from two study sites on the coast of southeast Queensland, Australia. Recordings were made from 2002 to 2014 at Peregian Beach (26°30' S, 153°05' E) and at Point Lookout on North Stradbroke Island (27°43' S, 153°53' E), as described in Chapter 3.

4.3.2 Song transcriptions

All recordings were assessed visually and aurally using Raven Pro 1.4 (www.birds.cornell.edu/raven). Spectrograms were generated (2048 FFT size, 90% overlap, Hann window) and recordings were inspected for quality. Those recordings with a signal-to-noise ratio (SNR) of at least 10 dB above the background noise were included in further analysis. Songs were transcribed at the unit level into numerical sequences using the acoustic dictionary created in Chapter 2. All songs transcribed in Chapter 3 were used for this study. Thirty-six complete song cycles were transcribed from each year from 2002 to 2014, excepting 2006 (12 song cycles) and 2007 (4 cycles) due to insufficient high-quality recordings. The nature of the migratory route means that individuals consistently travel past the study sites rather than spending time there (Noad and Cato, 2007; Horton *et al.*, 2011; Kavanagh *et al.*, 2017). Song cycles recorded on separate days

were therefore assumed to be separate individuals. In total, 412 complete song cycles from 95 singers representing 13 consecutive years of song recordings were transcribed.

4.3.3 Verification of theme classifications

The qualitatively assigned themes were verified quantitatively in Chapter 3 using the Levenshtein similarity index (LSI) (Garland *et al.*, 2012; Murray *et al.*, 2018). The LSI analysis was run as a weighted analysis based on the similarity in the acoustic features of units (see Chapter 2, Allen *et al.*, 2017). Qualitative theme classifications were confirmed using average linkage hierarchical cluster analysis and bootstrapping, which grouped each identified theme or theme variant onto a major dendrogram branch (see Chapter 3). All dendrograms had a cophenetic correlation coefficient (CCC) greater than 0.8 (see Chapter 3), indicating good representation of the associations within the data (Sokal and Rohlf, 1962).

4.3.4 Small-world network analysis

For each year, a network model was generated for the 36 song cycles from that year (12 cycles in 2006, 4 cycles in 2007), as well as for all years combined (2002 to 2014) using the complete set of 412 song cycles. Network analysis was performed using the *PajaroLoco* software package (Sanchez *et al.*, 2015) in Mathematica version 10.4. As sequential order of units was an important component of the analysis and needed to be accounted for, all models were run as directed networks which incorporate direction of transitions. Each network model quantified the connectivity among units (i.e., units which were adjacent in a sequence) in each dataset and compared it to a random network with the same number of units and connections as that dataset (Watts and Strogatz, 1998; Humphries and Gurney, 2008). This measure, termed the small-world coefficient (S), is calculated following Humphries and Gurney (2008) as:

$$S = \left(\frac{C}{C_{\text{rand}}}\right) \Big/ \left(\frac{L}{L_{\text{rand}}}\right)$$

where C is the clustering coefficient for the study dataset, L is the characteristic path length for the study dataset, and C_{rand} and L_{rand} are values for C and L calculated for a randomized dataset. The clustering coefficient (C) is an average measure of the extent to which a particular unit is connected to units that are also connected to each other (Humphries and Gurney, 2008; Bullmore and Sporns, 2009; Sasahara *et al.*, 2012). High C values occur when there are high numbers of connections among units. Characteristic path length (L) represents the average shortest distance (i.e., the number of steps required to connect two units) when connecting each unit to every other unit

(Humphries and Gurney, 2008; Bullmore and Sporns, 2009). To qualify as a 'small-world' network, the small-world coefficient (S) must be greater than 1 (Humphries and Gurney, 2008). Small-world networks are characterised by clusters of units known as 'small-world themes' which have a higher number of connections amongst each other than with units outside of the small-world theme (Watts and Strogatz, 1998; Humphries and Gurney, 2008).

4.3.5 Unit usage

For all of the song-cycles in a given year, units were ranked in ascending order based on the frequency of their occurrence in the dataset each year (i.e., the most frequently occurring unit was rank 1, the second most frequently occurring unit was rank 2, etc.). Rankings and frequency of occurrence were plotted logarithmically (log rank of use vs log frequency of occurrence), generating a distribution of unit usage for each year (Mandelbrot, 1961; Hailman *et al.*, 1985; Martins, 1994; Briefer *et al.*, 2010; Grimsley *et al.*, 2011) to determine how "open" the repertoire is. A repertoire with a slope of -1 (indicative of a Zipf Curve) has a balance of diversity and redundancy with a small number of sounds used very frequently and many sounds used infrequently (Zipf, 1949; Briefer *et al.*, 2010; Grimsley *et al.*, 2011; Deslandes *et al.*, 2014). A slope of less than -1 indicates a "closed" system which has more redundancy with a few specific units dominating use. A slope between 0 and -1 indicates an "open" system that has more diversity but less selectivity with many units that are used with similar frequency. The same calculation was repeated using all years combined based on the 412 song cycles. Frequency of occurrence and rank of use were calculated using the *PajaroLoco* software package (Sanchez *et al.*, 2015) in Mathematica version 10.4.

4.3.6 Transition motifs

The transition patterns or 'motifs' were based on the sequential arrangements of the units in the song cycles. For the 36 song cycles in a given year (12 in 2006, 4 in 2007), the number of unit types that preceded another unit were counted and then averaged across all unit types. The number of unit types that followed another unit were also counted and then averaged for the song cycles in each year (Sasahara *et al.*, 2012; Taylor and Cody, 2015). These averages were used to calculate the different transition patterns, which were divided into the following four categories as defined by Sasahara *et al.* (2012) (see Fig. 4.1):

1. Bottleneck – a greater than average number of unit types precedes and a less than average number of unit types follow
2. Hourglass – a greater than average number of unit types both precede and follow

3. Branch – a less than average number of unit types precedes and a greater than average number of unit types follows
4. One-way – a less than average number of unit types both precedes and follows.

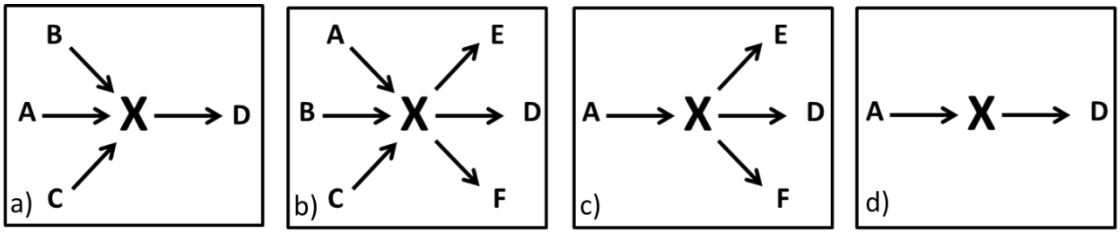


Figure 4.1 Diagrams representing the four types of transition motifs, adapted from Sasahara *et al.* (2012): a) Bottleneck, b) Hourglass, c) Branch, and d) One-way

Bottleneck and one-way motifs are 'deterministic', meaning that fewer than average units follow any particular unit type. Hourglass and branching motifs are 'non-deterministic', meaning that greater than average units follow any particular unit type (Sasahara *et al.*, 2012). The number of times each of the four transition motifs occurred was counted in each song cycle and the average occurrence of each motif was calculated for each year's dataset separately. All years were then combined and analysed as a single data set. Averages were calculated (as described above) from the combined dataset of all 412 song cycles. Based on these averages, a count of how many times each type of motif occurred was calculated. The proportions of deterministic and non-deterministic transitions were compared within each year and among all years using a paired Student t-test.

4.4 Results

There were 142 unit types in the song repertoire over the entire study period (2002 to 2014; Chapter 2). The average repertoire size for each year ranged from 21 to 73 unit types per year (Table 4.1) with an average of 45 unit types per year.

Table 4.1 Summary of data set for each year. Recordings were collected by a fixed hydrophone array (array), deployed autonomous recorders (recorder), or boat-based hydrophones (boat). 2006 and 2007 had small sample sizes due to a lack of high quality recordings. Themes refer to the total number of themes used in that year.

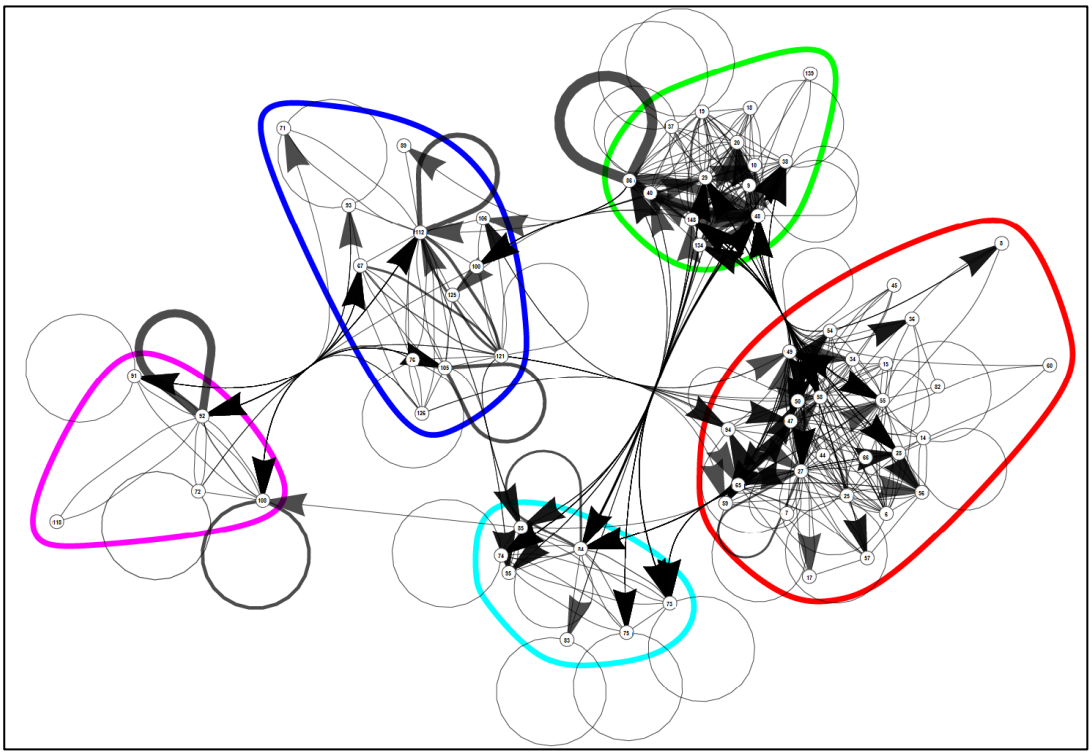
Year	Collection	Singers	Song Cycles	Themes	Repertoire
2002	Array	6	36	7	39
2003	Array	7	36	6	28
2004	Array	8	36	6	57
2005	Boat	7	36	5	56
2006	Boat	2	12	6	40
2007	Boat	1	4	4	21
2008	Array	9	36	6	55
2009	Array	6	36	3	44
2010	Array	8	36	5	65
2011	Array	9	36	4	67
2012	Recorder	13	36	7	73
2013	Recorder	9	36	5	48
2014	Array	10	36	5	41
All Years	NA	95	412	69	142

4.4.1 Small-world networks

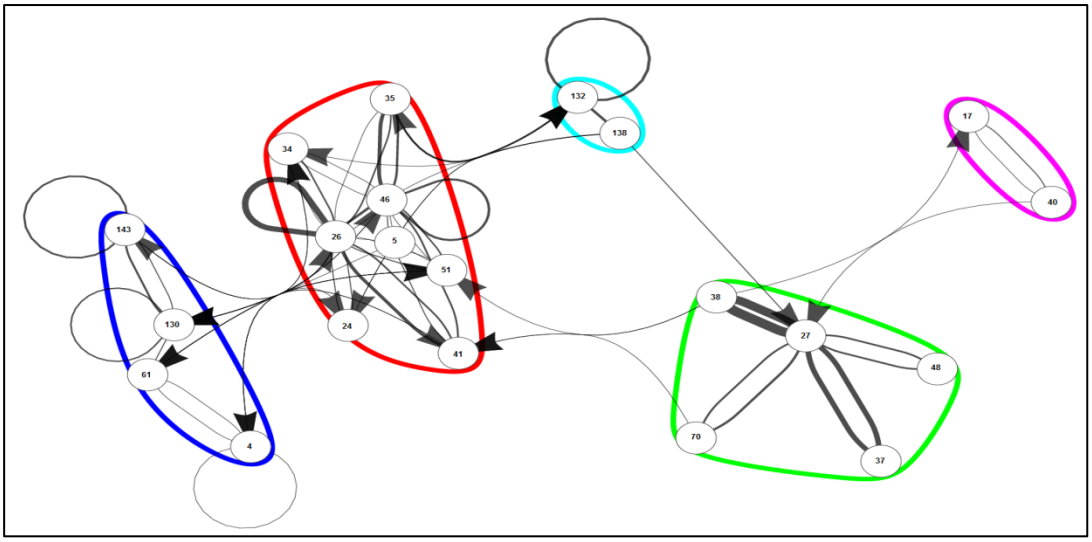
Directed network models were calculated for each year based on the 36 song cycles for that year (with only 12 in 2006 and 4 in 2007) (Fig. 4.2; see Table 4.2 for network features). Songs in every year had small-world network structure, with small-world coefficients (S) ranging from 1.2 to 5.1 with an average of 3.0 (Fig. 4.3, summary of small-world variables in Table 4.2). This means that in each year, song arrangements contained clusters of unit types which are often adjacent to one another in a song sequences ('small-world themes'), but any two unit types only need a few steps to connect them. For example, if the sequences "AB" and "ABB" both occur frequently in multiple song sequences, then A and B are highly connected and would be found in the same small-world theme. If the sequence "ABCDEF" occurs, there is a short distance between A and C (one step),

but there is a larger distance between A and F (four steps). Each year contained three to seven small-world themes (Appendix 3), but these did not correspond to the qualitatively identified song themes. An additional directed network model was created for all years combined based on the total 412 song cycles. The small-world coefficient for all year combined was 2.6 and had 12 small-world themes present (Fig. 4.2). Therefore, when song sequences were quantified regardless of what year or song type they came from, unit types still clustered into highly connected groups with short distances between unit types. Network structures were not significantly different between songs resulting from evolutionary transitions versus revolutionary transitions (Table 4.2, heteroscedastic t-test, $p>0.05$ for all features)

a)



b)



c)

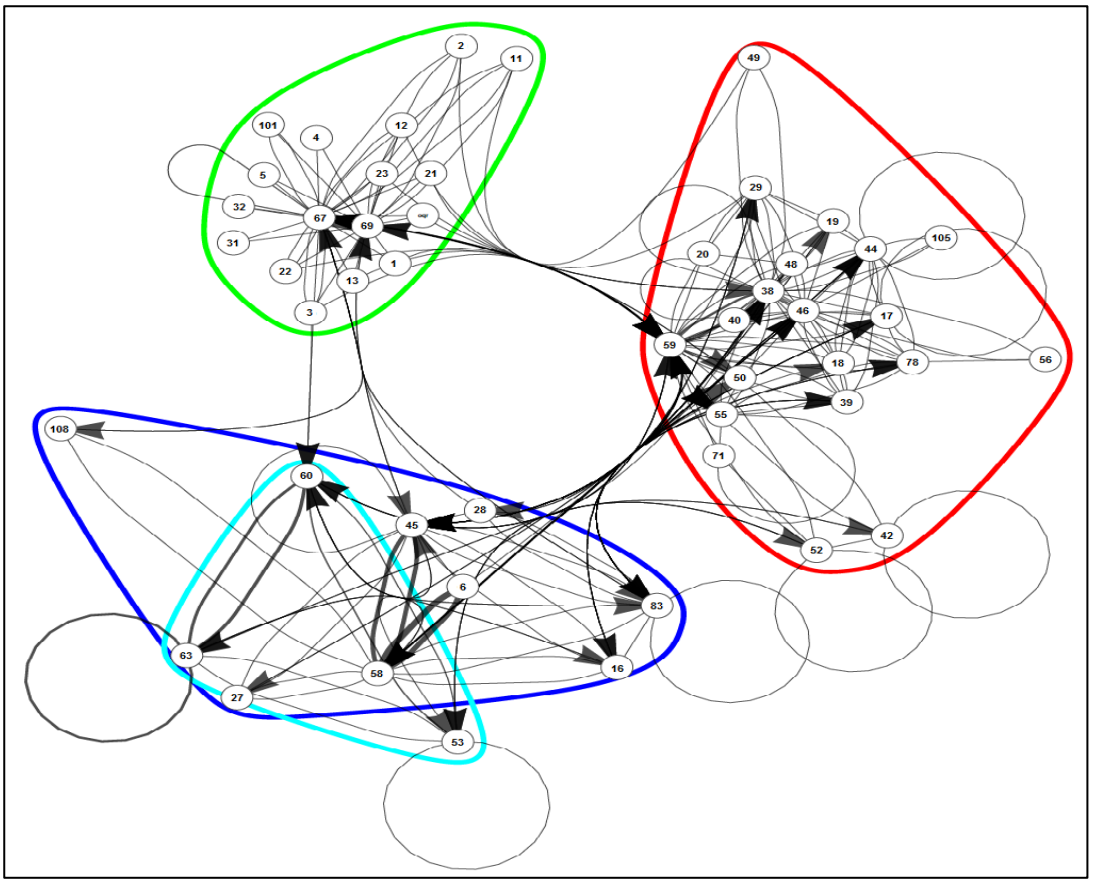


Figure 4.2 Examples of directed network representations of units for the song sequences for a) 2010, b) 2007, c) 2013. 2010 (S=3.1, N=36) provides an example with an average amount of small-world structure (average S=3.0). 2007 (S=1.2, N=4) and 2013 (S=5.1, N=36) each provide examples of the lowest and highest levels of small-world structure found in this study. Units served as the vertices and the transitions between units served as the directed edges (or connections) between vertices. Arrows indicate transition direction between units, and line thickness indicates the frequency of the transitions. There are high amounts of clustering between certain groups of units (the small-world themes) circled in different colours. Units within small-world themes have more transitions between each other than with units outside their own theme. Only a few transitions connect units between separate small-world themes. Network representations for each year (2002-2014) and for all years combined can be found in Appendix 3

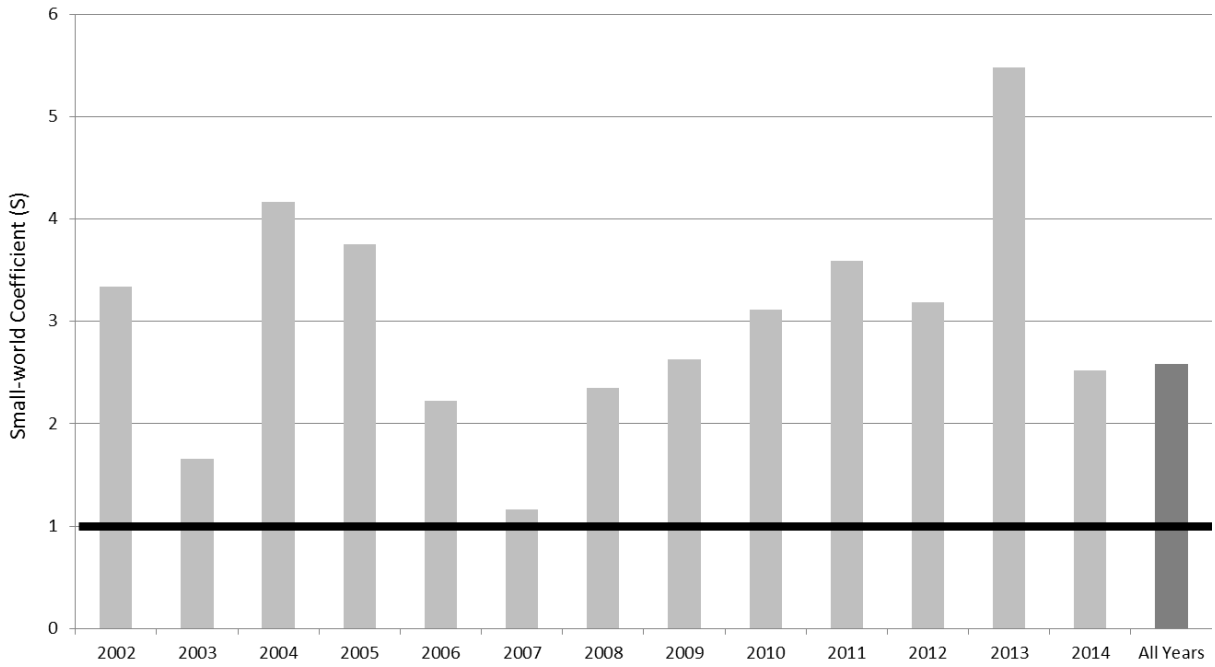


Figure 4.3 Small-world coefficient (S) values. S-values are shown for each year (average S=3.01) based on all of the song cycles for that year (N=12 in 2006, N=4, in 2007, N=36 per year 2002-2005 and 2008-2014; light grey bars), as well as the coefficient for all of the song cycles (412 for 2002-2014) in all years combined (dark grey bar). The black line marks the threshold for small-world topography (S=1.0).

4.4.2 Unit usage

The rank of unit usage was inversely correlated to the frequency of occurrence in each year (Appendix 3) and when all years were combined (Fig. 4.4). All graphs of log rank vs log frequency displayed a convex departure from linearity, with a slope that approached zero as the rank of use increased. The linear regressions had negative slopes with an average of -1.9 and ranging from -1.1 to -2.2 in each year. Therefore, the song repertoire for each year (and for the entire repertoire regardless of year) was composed of a few units used frequently with many units being used rarely. The negative slopes found here suggest that song repertoires contained more redundancy than diversity (Briefer *et al.*, 2010; Grimsley *et al.*, 2011).

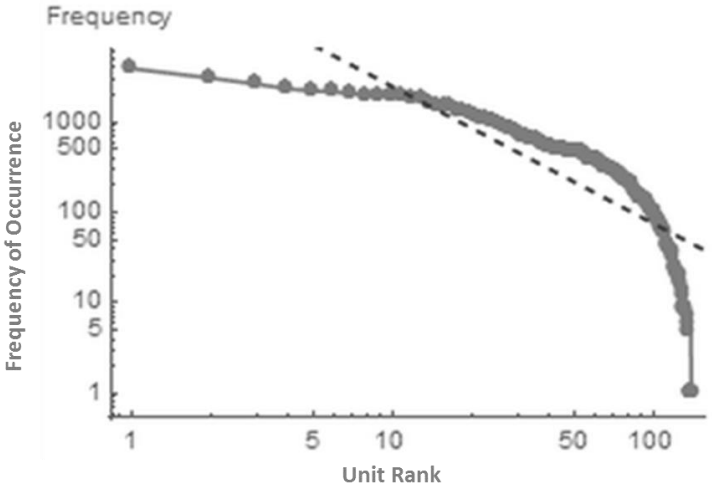


Figure 4.4 Unit usage distribution for all years combined. The logarithmic distribution of rank of unit use (x-axis) is modelled as a function of the frequency of occurrence (y-axis) for all units used across every song type in every year (N=412 song cycles). The dashed line represents the Zipf curve, which is linear with a slope of -1. Distributions for each year can be found in the Appendix 3

Table 4.2 Network features for each year and all years combined. Features include song type (whether a song resulted from evolutionary or revolutionary change), the small-world coefficient (S), path length (L), clustering coefficient (C), small-world themes, unit repertoire size, and slope of unit usage.

Year	Type	S	L	C	S-W Themes	Repertoire	Slope of Unit Usage
2002	Evolution	3.3	2.4	0.5	5	39	-2.2
2003	Revolution	1.7	2.1	0.4	5	28	-2.2
2004	Evolution	4.2	2.2	0.6	7	57	-1.9
2005	Evolution	3.8	2.4	0.6	5	56	-2.1
2006	Revolution	2.2	2.1	0.5	5	40	-1.6
2007	Revolution	1.2	2.3	0.3	5	21	-1.1
2008	Evolution	2.4	2.1	0.4	4	55	-2.1
2009	Revolution	2.6	1.8	0.7	5	44	-2.1
2010	Evolution	3.1	2.2	0.6	5	65	-1.9
2011	Revolution	3.6	2.2	0.6	3	67	-1.9
2012	Evolution	3.2	2.1	0.6	4	73	-1.8
2013	Revolution	5.1	2.0	0.7	4	48	-2.2
2014	Revolution	2.5	2.0	0.5	4	41	-2.1
All Years	N/A	2.6	1.9	0.6	12	142	-1.5

4.4.3 Transition motifs

Deterministic motifs (only a few units follow any particular unit) were significantly more common than non-deterministic motifs (many different units follow any particular unit) in each year's song (paired t-test for each year separately, all $p<0.01$). Most transition motifs in the song

arrangement each year were deterministic (average=59%, range 53-71%), except for 2006 which had equal proportions of deterministic and non-deterministic transitions (Fig. 4.5). When all years were combined, the percentages of deterministic and non-deterministic motifs were 64% and 36%, respectively. Deterministic motifs restrict which units can follow in a song sequence, limiting its variability to only a few options. Therefore, songs have approximately 1.5 as many transitions that indicate stability in the song's arrangement compared with non-deterministic motifs, which promote variability because they can be followed by many different unit types.

One-way motifs (where few units precede and follow a unit) were the most common motif, comprising approximately 45-65% of all transitions in any given year (Table 4.3). Hourglass motifs, which have high numbers of units both preceding and following a unit, were the second most common motif, comprising approximately 20-40% of transitions. Branch (few units precede a unit, but many units follow) motifs transition from stability to variability and bottleneck (many units precede a unit, but only a few units follow) motifs transition from variability to stability. These transitional motifs were far less common in each year, together contributing 5-20% of the total transition motifs. These trends in transition patterns mean that song sequences primarily contain sequences with either restricted patterns (one-way motifs) or variable patterns (hourglass motifs), but transitions from restricted patterns to variables ones (branch) or vice versa (bottleneck) were not common.

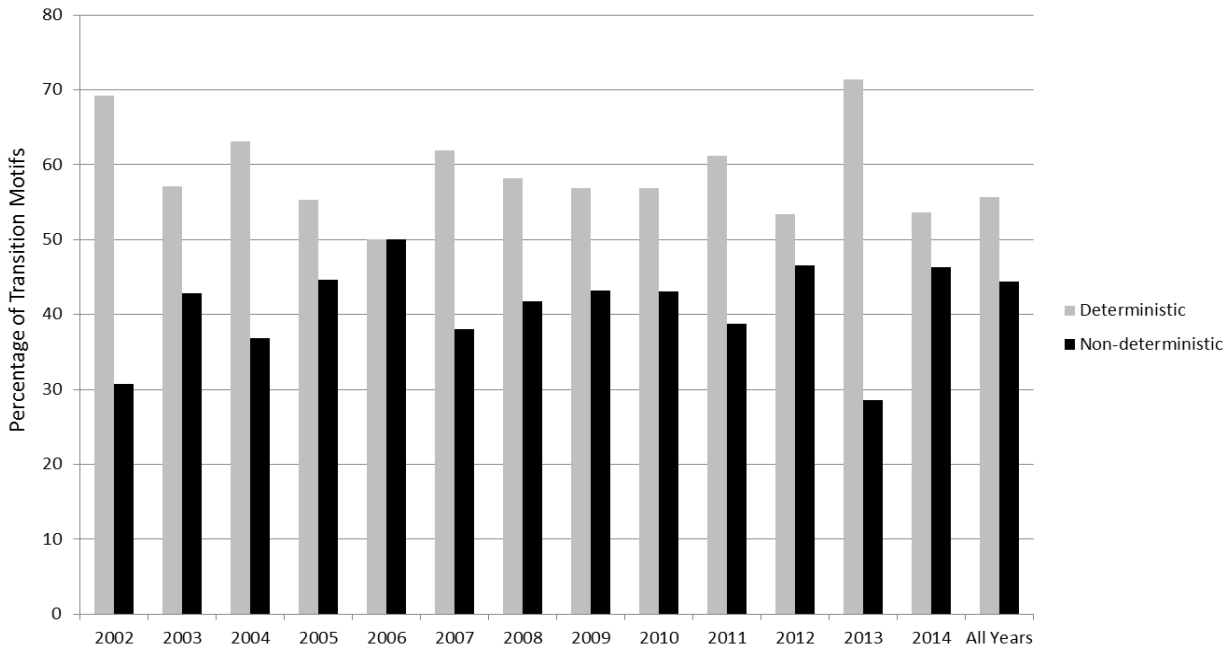


Figure 4.5 The proportion of deterministic or non-deterministic transition motifs. These are displayed per year, as well as for the transition motifs when all years were combined into a single network model

Table 4.3 Total number and percentage of transition motifs. Proportions of motifs are shown per year (N=36 song cycles for each year), as well as for the network model with all years combined (N=412 song cycles)

	Deterministic		Non-Deterministic	
Year	**One-Way**	**Bottleneck**	**Hourglass**	**Branch**
2002	24 (62%)	3 (8%)	8 (20%)	4 (10%)
2003	12 (43%)	4 (14%)	10 (36%)	2 (7%)
2004	33 (58%)	3 (5%)	13 (23%)	8 (14%)
2005	26 (46%)	5 (9%)	19 (34%)	6 (11%)
2006	18 (45%)	2 (5%)	12 (30%)	8 (20%)
2007	9 (43%)	4 (19%)	5 (24%)	3 (14%)
2008	29 (53%)	3 (5%)	18 (33%)	5 (9%)
2009	21 (48%)	4 (9%)	14 (32%)	5 (11%)
2010	33 (51%)	4 (6%)	23 (35%)	5 (8%)
2011	37 (55%)	4 (6%)	21 (31%)	5 (8%)
2012	35 (48%)	4 (5%)	30 (41%)	4 (6%)
2013	31 (63%)	4 (8%)	11 (23%)	3 (6%)
2014	19 (47%)	3 (7%)	12 (29%)	7 (17%)
All Years	74 (52%)	5 (4%)	54 (38%)	9 (6%)

4.5 Discussion

Humpback whale song contained several features that indicate a degree of structural complexity and syntax. Song patterns in every year (2002 to 2014) contained small-world network structure, meaning that unit types clustered into highly connected groups (small-world themes) with short distances between any pair of unit types. Small-world structure was also present when all years were combined into one network model. This indicates that highly connected units are a consistent feature in the general structure of the song display, rather than only found in each song type separately. Changes to small-world structure were not driven by changes to song arrangement since there were no significant structural differences between songs that underwent evolutionary versus revolutionary changes. Patterns in complexity or predictability of these song arrangements also had no significant relationship with small world structure over the study period (Pearson correlation coefficient, $p>0.5$ for both). Therefore, while song patterns and complexity changed each year (Garland *et al.*, 2011, Chapter 3), some degree of small-world structure was always

present in the song. This suggests that small-world structure is a feature of the humpback whale song display and not of any one arrangement.

Unexpectedly, each year's small-world themes (clusters of highly connected units) did not coincide with that year's identified song themes (the repeating and stereotyped patterns of units). Instead, unit types often occurred in more than one theme within a song rather than each theme containing a unique set of units. A similar pattern was seen when all years were combined into one network model: small-world themes of the multi-year network did not coincide with each year's song type. Unit types occurred across multiple years, regardless of whether songs had evolved or were unrelated due to a cultural revolution event. This verifies that even unrelated song types did not have entirely unique repertoires, but instead shared some unit types. Shared units between both themes and unrelated song types may encourage song learning because not every unit type will be novel, even when the song arrangement has been entirely replaced.

How unit types are arranged within the network structure showed common song features to be versatile in some aspects and restricted in others. This dichotomy stemmed from the two most common motifs in each year: one-way (few unit types precede or follow) and hourglass (many unit types precede or follow). One-way motifs indicate that many unit types "direct" the song pattern towards a specific sequence and limit its variability (Table 4.3). These units were typically found on the periphery of the small-world networks due to how few unit types they connected with. Conversely, hourglass motifs demonstrate the common use of some units as 'hubs' or points of high connection that facilitate variability in unit sequences (Weiss *et al.*, 2014). Their role as hubs of connectivity between many other unit types placed hourglass units at the centre of the small-world themes within each year's network. While there were more one-way unit types in the repertoire, hourglass unit types occurred more frequently in song sequences themselves. Therefore hourglass units were those few units found at the top of the unit usage curve, while one-way units were in the large group of lesser used units in the lower portion of the curve (Fig. 4.4). Hourglass units were primarily low frequency (~300-500Hz), flat, tonal calls such as "moans", "groans" or "cries", while one-way units covered the spectrum of acoustic features. The dominant use of these one-way (i.e. stable) and hourglass (i.e. diverse) transitions reflects the combination of stereotypy and variability that is observed in multiple levels of humpback whale songs (Payne and McVay, 1971; Sasahara *et al.*, 2012; Cholewiak *et al.*, 2013; Murray, 2015). Presence of these patterns across unrelated song types further suggest that they have fixed roles in the song structure. The common use of a few

hourglass units may allow incorporation of novelty by individuals, while the range of one-way units support stability in that year's general arrangement which all singers must conform to.

Repetitions were another particularly common pattern across song types, shown as loops within the network structures (Fig. 4.2). Doublet, triplet, and alternating repetitions frequently occurred for the wide range of one-way unit types, while longer bouts of multiple repetitions were mainly short duration, low frequency broadband calls such as "grunts" or "croaks". Call types making up these longer bouts typically served as one-way motifs because the unit was most frequently preceded and followed by itself. Both Payne *et al.* (1983) and Guinee and Payne (1988) found repetitions to be common through fine-scale qualitative song analyses. The prevalence of repetitions quantified here within the small-world structures of all song types supports the suggestion by Guinee and Payne (1988) that repetitions may aid in song learning by making songs easier to remember.

Overall, song structure featured stability and stereotypy by having approximately 50% more deterministic motifs (e.g. one-way and bottleneck) than non-deterministic motifs (e.g. hourglass and branching) in their arrangements. These deterministic motifs are associated with stereotypy by limiting the types of units that follow them, thus restricting variation in the song sequences (Sasahara *et al.*, 2012). The use of unit types within the song always followed a similar distribution to that found in all human languages (Zipf, 1949). In other words, each song type contained sequences with a few unit types that were commonly used while most units were rare. However, all plots were convex rather than linear, with linear regression slopes that were less than -1 (-1.1 to -2.2). Therefore, a better fit for the observed trend is the modified 'Zipf-Mandelbrot' curve, often observed in animal vocal displays (Mandelbrot, 1961; Briefer *et al.*, 2010; Koplenig, 2015). The Zipf-Mandelbrot trends found in this study (slope of unit usage, Table 4.2) indicate that each song's repertoire contains a lot of redundancy likely due to its repetitive hierarchical structure. Hourglass unit types such as moans, groans, or barks were disproportionately common in their usage compared to the rest of the repertoire. High usage of these few central units encouraged small variations within the stereotyped song sequences, which was how the remaining majority of units in the repertoire were used. Although following Zipf's law is not sufficient evidence of language, it does illustrate a certain amount of complexity within the organisation of the animal's vocal repertoire (McCowan *et al.*, 2005).

The same syntactic features identified in humpback whale song (small-world structure, deterministic motifs, and redundant unit usage) also occur in the songs of certain oscine bird species (Briefer *et al.*, 2010; Sasahara *et al.*, 2012; Deslandes *et al.*, 2014; Weiss *et al.*, 2014; Taylor and Cody, 2015; Cody *et al.*, 2016; Hedley, 2016). Small-world coefficient values in humpback whale songs were comparable to those seen in birdsongs studied with network analysis (S=1.69-4.3 for seven different species, summarized in Table 4.4). Reflecting network structure, deterministic transition motifs also occurred in similar proportions across these species. One-way transitions are the most commonly used motif, followed by hourglass "hub" elements which are central in the small-world structure (Table 4.4). Such parallels indicate that the network structures of these displays cluster their song elements (units in humpback whales, phrases in birds) in similar ways and encouraging stability in their song arrangements with predominantly deterministic motifs. Stability through small-world structures may therefore be taxon-general based on their presence in the vocal learning displays of multiple species.

Table 4.4 Network features in seven bird song displays compared with humpback whale song as analysed here (averaged over all 13 study years). S=small-world coefficients are given, as well as each of the four transition motifs (one-way, hourglass, bottleneck, branch). All transitions are given as percentages of the total number of transitions found in those displays. [1]Taylor and Cody, 2015; [2]Cody *et al.*, 2016; [3]Weiss *et al.*, 2014.

Species	**S**	**Deterministic**		**Non-Deterministic**	
		One-way	**Bottlenecks**	**Hourglass**	**Branches**
Western tanager[1]	2.10	57%	0%	43%	0%
Cassin's vireo[1]	4.70	38%	21%	26%	15%
Black-headed grosbeak[1]	2.70	34%	18%	25%	23%
Redthroat[1]	4.10	55%	7%	32%	5%
Sage thrasher[1]	2.86	62%	10%	20%	9%
CA thrasher[1]	2.60	51%	3%	27%	19%
CA thrasher[2]	1.69	50%	7%	32%	11%
Nightingale[3]	4.29	35%	15%	35%	14%
Humpback whale	3.00	51%	11%	27%	12%

Small-world structure is also found in human language (Cancho and Solé, 2001; Koplenig, 2015). Evidence suggests that small-world structure results from the need for language to have

'optimal navigation', in which words can be arranged to express an intended message efficiently using the smallest number of steps (Ferrer i Cancho and Solé, 2001; Capitán et al., 2012). While humpback whale songs do not contain information in the same way as human language, the consistent presence of small-world structure is likely to increase the efficiency of song learning. This could possibly explain how singers learn a song's pattern so quickly, as well as the song's ability to spread through an entire population within a single year or across a large spatial scale as shown in the South Pacific meta-population (Garland *et al.*, 2011).

Clarifying network structure provides additional evidence towards the established link between neurobiology and vocal learning (Doupe and Kuhl, 1999; Airey and DeVoogd, 2000; Zeigler and Marler, 2004; Brenowitz and Beecher, 2005; Petkov and Jarvis, 2012). Based on the presence of small-world structure in brain connectivity (Sporns *et al.*, 2004; Achard *et al.*, 2006; Reijneveld *et al.*, 2007; Bullmore and Sporns, 2009), Weiss *et al.* (2014) hypothesised that these neuronal networks should demonstrate parallels with song networks in terms of their small-world structure. I further suggest that these parallels would facilitate the rapid vocal learning seen in humpback whale song (Noad *et al.*, 2000; Garland *et al.*, 2011).

The current study quantifies the fine-scale structural complexity and syntactic patterns of humpback whale song. Although similar network modelling has been applied to birdsong (Sasahara *et al.*, 2012; Deslandes *et al.*, 2014; Weiss *et al.*, 2014; Taylor and Cody, 2015; Cody *et al.*, 2016; Hedley, 2016), it has not been previously applied to a mammalian song or to a hierarchical display. By filling these gaps using humpback whale song, the complex vocal learning displays of multiple species can be compared. Convergence of small-world structure occurs in the arrangements of complex birdsongs (Hedley, 2016). Its presence in humpback whale song indicates that this convergence occurs in complex songs across multiple vocal learning species. While these vocal displays may serve different functions within their respective species, they share a common need for individuals to learn them efficiently. If small-world structure does facilitate learning, then it is likely to be an important feature of vocally learned displays. The ability to learn syntactic rules for syllable arrangement is a fundamental component of vocal learning and development in humans (van Heijningen *et al.*, 2009; Feher *et al.*, 2016), birds (Romberg and Saffran, 2010), and humpback whales (Garland *et al.*, 2017a). Studies that quantify syntactic rules across distantly related species are therefore invaluable for understanding the origin and evolution of vocal learning and language.

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5 CHAPTER 5 Did you get that? Fine-scale analysis of humpback whale song between neighbouring populations reveals insights into cultural learning mechanisms.

5.1 Abstract

Cultural transmission between entire populations is rare among animal species. One of the few examples of inter-population cultural transmission is the song of male humpback whales (*Megaptera novaeangliae*). In the South Pacific, song transmission occurs eastward across populations in the region, with songs retaining their patterns in a recognizable way. Fine-scale analyses of sound 'unit' sequences in these songs are required to understand what specific features are important to inter-population song learning. This study quantified fine-scale features in the arrangement and structure of unit patterns for two distinct song types during the consistent cultural transmission from east Australia to New Caledonia. Four features of each song type were quantified between the two populations: 1) similarity in the song unit sequences, 2) song complexity, 3) second order information entropy, and 4) network structure. These features will help to determine how accurately song arrangements and structures were transmitted. There were no population-specific versions of either song type. Sound unit patterns remained consistent during inter-population transmission. Specific 'theme' arrangements of stereotyped unit patterns retained their complexity during transmission from east Australia to New Caledonia. These results suggest that complex song arrangements are learned without being simplified during inter-population exchange. Maintaining fine-scale features with such accuracy suggests that learning requires significant acoustic contact, supporting the hypothesis that high-fidelity song learning may occur on shared feeding grounds or migration routes. This study provides insight into the learning mechanisms of inter-population cultural transmission and broad-scale cultural learning in animal species.

5.2 Introduction

Cultural learning, once thought to be uniquely human, is found in a wide range of animal species. Individuals acquire a specific behaviour or trait through contact with another individual, known as social learning (Rendell and Whitehead, 2001; Whiten, 2009). Cultural transmission of these behaviours can occur between related individuals (e.g., tool use in a matriline of bottlenose dolphins [*Tursiops truncatus*]; Krützen *et al.*, 2005) social groups (e.g., sweet potato washing in a tribe of Japanese macaques [*Macaca fuscata*]; Kawai, 1965), or populations (e.g., geographically distinct birdsong dialects; Slater, 1986). Primates and cetaceans demonstrate a particularly varied and complex set of cultural traits, surpassed only by those found in humans (Whiten, 2009; Whitehead and Rendell, 2014). Importantly, studies on cetaceans provide an opportunity to examine culture and the processes that lead to cultural traditions and their transmission in a non-primate lineage. Humpback whales (*Megaptera novaeangliae*) are a good model species for investigating cultural exchange due to the presence of cultural traits in multiple aspects of their ecology. These include novel foraging strategies (Allen *et al.*, 2013), maternally directed site fidelity (Baker, 1986; Clapham, 1996; Calambokidis *et al.*, 2001; Garrigue *et al.*, 2011a; Rosenbaum *et al.*, 2017), and a complex song display (Payne and McVay, 1971; Noad *et al.*, 2000; Garland *et al.*, 2011).

A clear example of broad-scale cultural exchange among multiple populations is the transmission of humpback whale song within the South Pacific meta-population (Garland *et al.*, 2011). Song patterns are transmitted eastward from the east Australia population first to New Caledonia, Tonga, and American Samoa, and then onto the Cook Islands, and French Polynesia (Garland *et al.*, 2011). However, the learning mechanism(s) for this transmission are not fully understood. Payne and Guinee (1983) proposed three possible vectors for song transmission between populations: 1) inter-population movement of individuals between seasons, 2) inter-population movement of individuals within a season, or 3) acoustic contact along migratory routes or feeding grounds shared between populations. Movement between populations within either migratory or breeding seasons (June-November) in the South Pacific region is rare, but has been documented (Garrigue *et al.*, 2002; Garrigue *et al.*, 2011a). More commonly reported are inter-population movements between seasons (Garrigue *et al.*, 2011a; Garrigue *et al.*, 2011b), shared migratory routes (Constantine *et al.*, 2007; Steel *et al.*, 2008), and singing on the Antarctic feeding grounds (Stimpert *et al.*, 2012; Garland *et al.*, 2013a), presenting plausible mechanisms of transmission for the South Pacific. However, not all populations necessarily use the same mechanisms of song exchange. Movement of entire song patterns across multiple populations, as

observed in the South Pacific, has not yet been documented in any other location worldwide (Garland *et al.*, 2011; Garland *et al.*, 2015), or any other species except our own.

Humpback whale song is a long, complex vocal display produced solely by males (Payne and McVay, 1971). Individual sounds called 'units' are arranged in a sequence, which is termed a 'phrase' (Payne and McVay, 1971; Cholewiak *et al.*, 2013). Phrases are repeated multiple times to create a 'theme'. Themes are then sung in a consistent order without repetition, creating a 'song'. The song evolves over time through small, progressive changes, which all singers adopt through social learning (Payne *et al.*, 1983). These changes result in each year's song containing a slightly different arrangement, known as a 'song type'. Related song types form a 'song lineage'. In the east Australian population, the progressive changes tend to increase song complexity during evolutions (quantified using 'complexity scores'; Chapter 3). For example, songs increase in duration, new themes are added, and a wider variety of units are used as songs evolve. Following these evolutionary changes, songs may also undergo a radical population-wide change known as a 'revolution', where a different song type introduced from the west Australian population entirely replaces the existing song (Noad *et al.*, 2000). Revolutionary songs tend to have lower complexity than the songs they replace, possibly as a result of limitations in learning such a large amount of novel material (Chapter 3).

In addition to the song's well-established hierarchical structure (Payne and McVay, 1971) and variable features such as song complexity (Chapter 3), several additional fine-scale features have recently been quantified in the east Australian song (Chapter 4, Murray et al., 2018). While nested hierarchy describes the multi-level structure of song (i.e. units comprise phrases, which comprise themes), network structures describe how units are used within sequences (i.e., which units are used, how often, and in what combinations). Song units are consistently arranged into a 'small-world' network structure (Chapter 4). Small-world networks are characterised by clusters of highly connected signals (i.e., signals that are frequently adjacent to one another in an arrangement) and suggests a degree of complexity in the rules governing sequential arrangement (Watts and Strogatz, 1998; Cancho and Solé, 2001; Cody *et al.*, 2016). The presence of small world structure remained consistent in east Australian humpback whale songs over a 13-year period (Chapter 4). Along with the nested hierarchy found in songs from every humpback whale population (Payne and McVay, 1971; Cholewiak *et al.*, 2013), these fine-scale network structures are fixed in the east Australian song display regardless of the song's pattern.

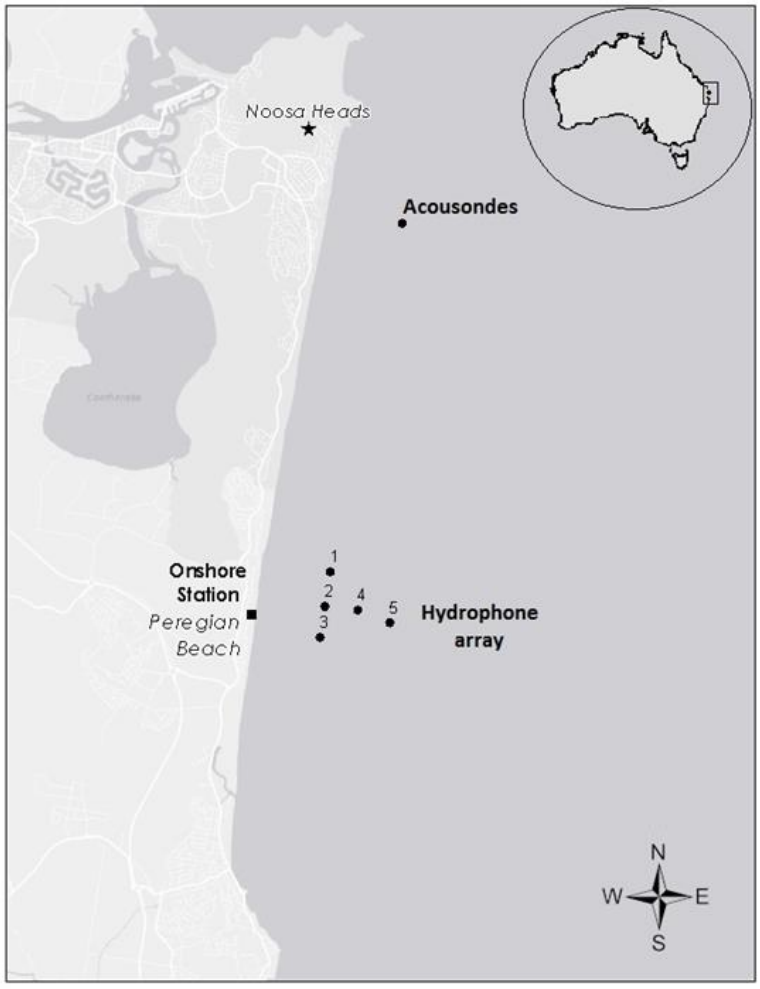
Among the South Pacific humpback whale populations, the song of the east Australian population is particularly well-studied (Noad *et al.*, 2000; Smith, 2009; Garland *et al.*, 2011; Allen *et al.*, 2017; Murray *et al.*, 2018). There is a consistent one-year delay in song transmission from east Australia to its closest neighbouring population, New Caledonia (Garland *et al.*, 2011; Garland *et al.*, 2013). Although a one-year transmission in song also occurs from the west Australian population to east Australia with the same eastward directionality, this is intermittent and has only been documented in 'revolution' years (Rekdahl, 2012a). The inter-population transmission across the South Pacific has strong song similarity on a broad scale (i.e., the sequences and occurrences of themes) (Garland *et al.*, 2011). Understanding fine-scale similarity in song patterns and structural features will clarify how song transmission impacts song structure at the unit-sequence level.

Fine-scale features of unit sequences in the east Australian humpback whale song were quantified in Chapters 3 and 4. The current chapter extends these analyses to a second population to explore how previously identified features such as fluctuating complexity or information entropy (Chapter 3) and small-world structure (Chapter 4) are affected by inter-population transmission. Identifying commonalities across populations will provide a baseline understanding of inter-population song learning mechanisms in humpback whales at a finer scale than previous works. Here, we analysed two distinct and unrelated song types that were first recorded in the east Australia population and subsequently transmitted to the New Caledonian population the following year causing a song revolution each time. This allowed for a direct and fine-scale comparison of song features using the same song patterns sung by two separate populations, where an unrelated song with large amounts of novel material is introduced. Following the results of Chapter 3, it is hypothesised that the New Caledonian versions of each song type will be simplified compared to their east Australian counterparts, as a means to facilitate song learning when large amount of novel material are presented during directional song transmission during these revolution events. I further hypothesise that song types will retain comparable degrees of small-world structure during inter-population transmission. Therefore each song type should be simplified when learned by the males in New Caledonia, but retain the same degree of small-world structure, implying that underlying structures can be learned and maintained more easily than the specific patterns of the displays.

5.3 Methods

5.3.1 Data collection

Data were collected from two sites (Fig. 5.1): Peregian Beach on the coast of southeast Queensland, Australia (26°30’ S, 153°05’ E), and the southern lagoon of New Caledonia (22°28’ S, 166°56’ E). Passive acoustic recordings in east Australia were collected in 2013 and 2014 using two autonomous loggers (Acousonde 3A with external battery housings, Greenridge Sciences) and a fixed five-buoy hydrophone array (detailed in Chapter 2, Fig. 5.1a). New Caledonian recordings were made off the southern coast of New Caledonia. A single passive acoustic recorder (SM2M+ Whalesong recorder, Wildlife Acoustics) was deployed each year from July-September in 2014 and 2015 at ~60 m depth (Fig. 5.1b). The SM2M+ recorder (SMX-II microphone with a sensitivity of −160 dB [+/- 4dB], and flat frequency response of 20 Hz–20 kHz) was programmed with an 18-hour duty cycle (hours: 1500 to 0900 the following day) at a sampling rate of 22 kHz, a high-pass filter of 3 Hz, and gain of 30 dB. Files were stored in WAC0 format on a 128GB SD card. These files were then converted to WAV format using Kaleidoscope Analysis software (Wildlife Acoustics).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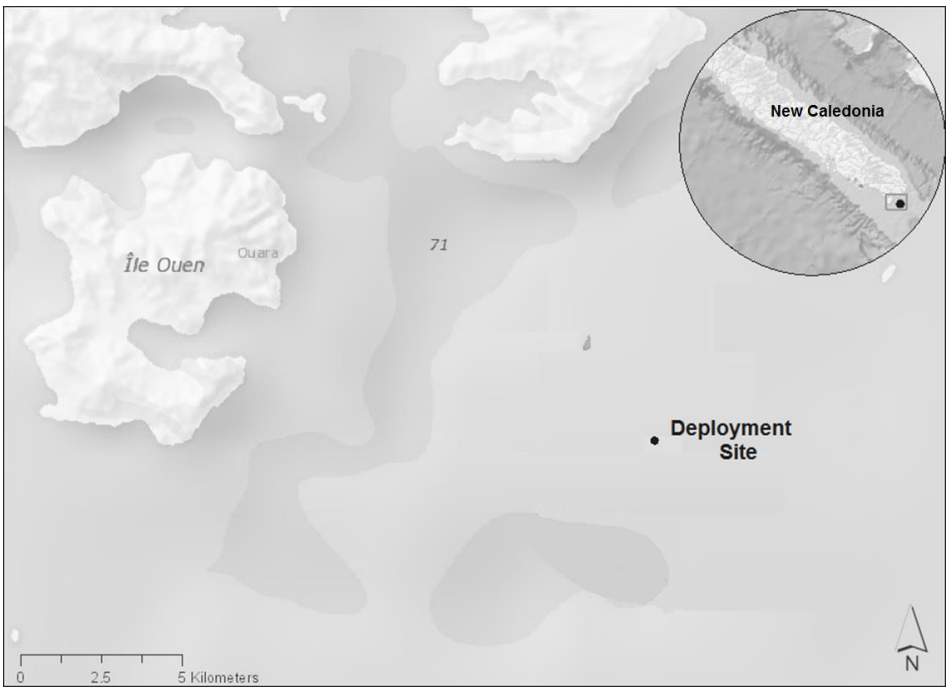
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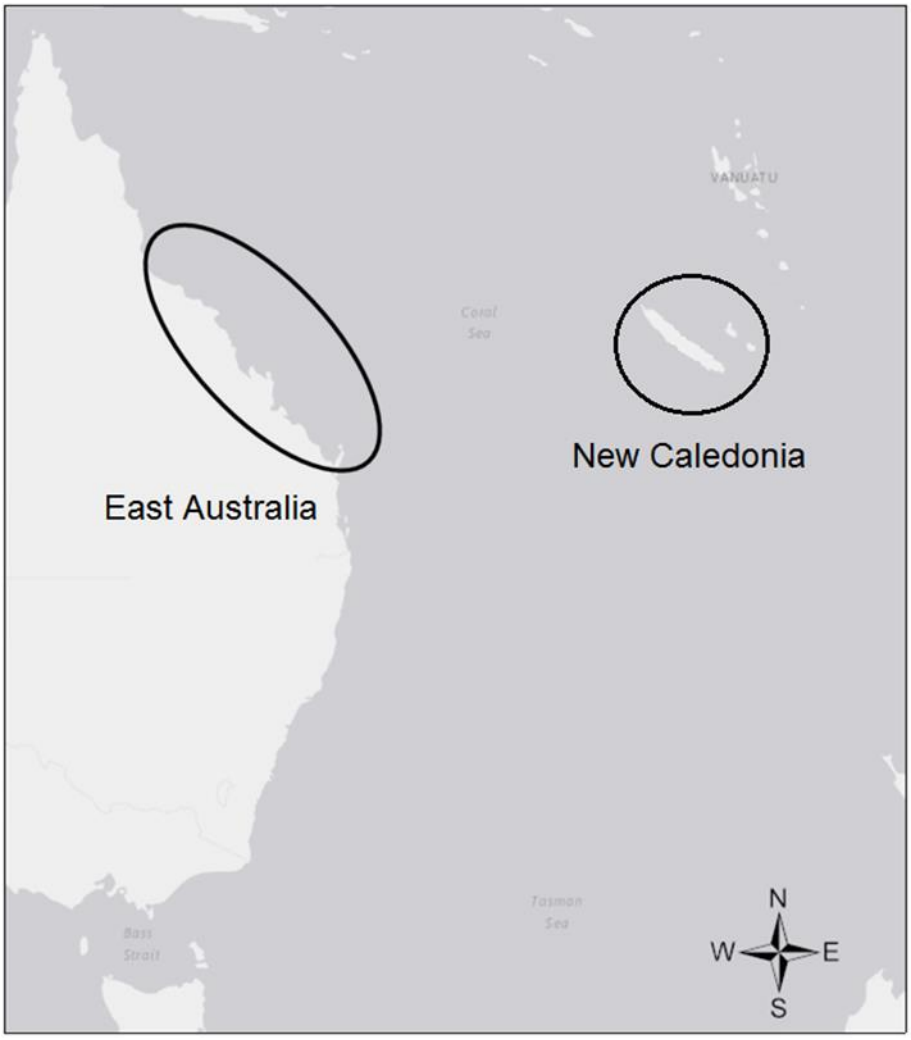


c)

Figure 5.1 Map of study sites in a) east Australia and b) New Caledonia. Figure 1a shows the placement of the Acousonde autonomous recorder deployments and the hydrophone array (buoys numbered 1-5) in east Australia. Figure 5.1b shows the placement of the SM2M+ recorder deployment in New Caledonia. Figure 1c shows the two populations in relation to one another.

5.3.2 Song transcriptions

Spectrograms were generated in Raven Pro 1.4 (www.birds.cornell.edu/raven) and evaluated for quality following the methods outlined in Chapter 2. Song patterns were transcribed at the individual sound unit level using an acoustic dictionary (following Chapter 2). Thirty-six complete song cycles were transcribed per year for each population, resulting in 144 complete song cycles taken from 24 singers (six singers in each year). Song cycles were considered to be from separate individuals if they were recorded on separate days. Although a small portion of singers in New Caledonia were recorded singing the previous year's song, they were excluded from this study to focus on fine-scale comparisons between the same song pattern sung by the separate populations.

5.3.3 Verification of theme classifications

Qualitative theme assignments were quantitatively verified for each population separately, following the Levenshtein distance similarity index (LSI) analysis in Chapter 3 (Garland *et al.*, 2012; Murray, 2015). The calculation was weighted based on the acoustic feature similarity of units (Garland *et al*., 2017b; Chapter 2; Allen *et al.*, in press). The LSI values were calculated between every pair of phrases (each phrase is composed of a sequence of units). Initially, the song from each population in each year was evaluated separately to identify the themes present and assign these to a song type. The same song types from each population were then grouped together for comparison and assigned a colour name (Teal song type: east Australia 2013 and New Caledonia 2014; Orange song type: east Australia 2014 and New Caledonia 2015). This allowed themes to be assigned to each song type irrespective of population. Once assigned to a common theme label, population differences within each theme could be analysed. The LSI matrix was clustered using average-linkage hierarchical clustering and bootstrapping using *pvclust* and *hclust* packages in *R* (Suzuki and Shimodaira, 2006) and custom written code (available at https://github.com/ellengarland/leven).

5.3.4 Similarity analysis

To characterise each theme's pattern of units, a representative phrase of each theme was needed. This was accomplished by creating a "set median" or the most representative phrase for each theme in every song cycle (N=36 song cycles per year per population, total N=144 song cycles). The set median is defined as the phrase that had the lowest sum of Levenshtein distances between itself and every other phrase of that theme (i.e., it had the highest overall similarity to all of the other phrases of that theme) (Kohonen, 1985; Helweg *et al.*, 1998; Tougaard and Eriksen, 2006; Garland *et al.*, 2015). The sequence of units from each set median phrase were then arranged to reflect the sequence of themes in each respective song cycle. Set median sequences were generated for each song cycle in the dataset, providing a representative pattern at the unit level of each song cycle (see Table 5.1 for example set medians) without the repetition of the phrases. This resulted in 144 representative song-cycles that were composed of the set medians of each theme for that particular song cycle knitted together. First, the LSI was calculated between every pair of set median song cycles (N=144) to verify the qualitative assignment of the two song types. To identify any population-level differences within each song type, separate similarity analyses were also conducted between every pair of set median song cycles per song type (Teal: N=72, Orange: N=72; examples in Table 5.1).

Table 5.1 Example song cycles composed of knitted together theme set medians (unit sequences). Each unit type is represented by a number (taken from the acoustic dictionary presented in Chapter 2). Units occurring in repetitive bouts were indicated by an "x" followed by the number of repetitions of the preceding unit. Brackets have been added to demarcate each theme and were not included in analyses. As shown, each complete song cycle (N=144) was generated by knitting together the respective theme set medians taken from that particular song cycle. This removed phrase repetitions from the analysis. Examples were randomly selected from the 36 song cycles in each song type/population.

Song Type	Population	Song cycle #	Song cycle composed of set median unit sequences
Teal	East Australia (2013)	8	[59, 6 83, 6, 45, 6] [59, 45, 38, 45, 45, 38] [59, 69, 67, 69, 67, 69, 67, 69, 67] [59, 42, 42] [60, 63, 63]
		30	[59, 6, 45, 6, 45, 6, 44, 6] [59, 39, 83, 45, 39] [59, 69, 67, 3, 69, 67, 3, 69, 67, 3, 69, 67, 3] [59, 42, 42, 60, 63, 63]
	New Caledonia (2014)	38	[59, 58, 6, 58, 45, 58, 6, 58, 46, 46, 58, 6, 58, 16] [59, 38, 45, 38] [59, 57, 67, 57, 67, 57, 67, 69, 67, 11, 69, 67] [60, 52, 42] [60, 53, 53]
		71	[59, 58, 6, 58, 45, 58, 6, 58, 45, 58, 6, 58, 45, 58, 45, 58, 16] [59, 38, 45, 45, 38] [59, 57, 67, 57, 67, 57, 67, 57, 67, 57, 67] [59, 42, 52] [60, 53, 53]
Orange	East Australia (2014)	75	[20, 69, 14, 133, 133, 69, 34, 133, 133, 69, 34] [20, 75, 75, 75, 84] [20, 138, 138]
		95	[48, 69, 34, 127, 127, 69, 14, 127, 127, 69, 34] [20, 75, 75, 75, 75] [20, 134, 134, 134, 134, 134, 134, 134] [48, 126(x34)]
	New Caledonia (2015)	113	[20, 69, 14, 133, 50, 54, 133, 50, 34] [20, 75, 55, 75, 75] [20, 111, 132, 132, 132, 132, 132, 132] [75, 69, 126(x26)]
		140	[20, 69, 14, 133, 133, 69, 14, 133, 133, 69, 14] [20, 75, 75, 85, 85] [20, 111, 111, 111, 134, 134] [20, 126(x32)]

5.3.5 Complexity scores

Song complexity was evaluated using two 'complexity scores' generated for each year's song following the methods presented in Chapter 3, modified from Boogert *et al.* (2008) and Templeton *et al.* (2014). Complexity scores were generated by reducing positively correlated variables to a single principal component using principal component analysis (PCA). *Song* level scores represented the full sequence of units in the song cycle, including all phrase repetitions, using the following variables: number of units per song cycle, number of unit types per song cycle, and duration of each song cycle (s). *Theme* level scores accounted for the presence of separate

themes using the following variables: number of themes per song cycle, mean phrase duration per song cycle (s), and mean individual theme complexity score per song cycle (calculated following Chapter 3). Scores have a direct, positive relationship with complexity: higher scores indicated higher complexity within the song. To further evaluate population-level differences, a set of complexity scores was also calculated for each individual theme per population for comparison. Differences in separate theme complexities between the two populations were then evaluated using a non-parametric Mann-Whitney/Wilcoxon test (sample sizes in Table 5.2). Statistical analyses were run in *R* (Version 3.3.0, R Core Development Team, 2016).

Table 5.2 Sample size of the number of phrase repetitions for each theme

Song Type	Population	Theme	Sample Size
Teal	East Australia (2013)	**EA13A**	151
		EA13B	269
		EA13C	200
		EA13D	86
		EA13E	350
	New Caledonia (2014)	**NC14A**	97
		NC14B	90
		NC14C	124
		NC14D	119
		NC14E	163
Orange	East Australia (2014)	**EA14A**	364
		EA14B	147
		EA14C	157
		EA14D	78
		EA14E	43
	New Caledonia (2015)	**NC15A**	415
		NC15B	136
		NC15C	134
		NC15D	14
		NC15E	20

5.3.6 Information entropy

As demonstrated in Chapter 3, second-order entropy estimates can quantify humpback song sequence predictability (Shannon, 1948; McCowan *et al.*, 1999). A low estimate indicates a predictable arrangement while a high estimate indicates a randomised arrangement. Two separate entropy estimates were calculated for all song cycles in each year and population: theme sequences (i.e., the order in which the themes were arranged) and unit sequences (i.e., the entire arrangement of units in the song cycle). Entropy estimates were calculated using the following equation:

$$H_2 = -\sum_{i,j}^{N} P(i)P_i(j)\log_2 P_i(j)$$

Where *P(i)* is the probability of occurrence of element *i*, *Pi(j)* is the probability of occurrence of unit *j* given the preceding unit is element *i*, and *N* is the number of elements (types of units) in the repertoire (Shannon, 1948).

5.3.7 Network analysis

Network features were calculated following the methods described in Chapter 4. All network analyses were performed using the *PajaroLoco* software package (Sanchez *et al.*, 2015) in Mathematica version 10.4 (Wolfram Research Inc, 2016). Directed network models were generated for each year and population (N=36 song cycles for each year/population for a total of four models), including all phrases. Each of the four models quantified the connectivity among units (i.e., adjacent units in a sequence) within each song type in each population to determine the song's network structure. 'Small-world' networks are comprised of highly connected units that only have a few steps between them. Highly connected units are those that frequently occur adjacent to each other in song sequences. To illustrate this in the context of song patterns, consider the sequence ABC: unit A and unit B are connected, unit B and unit C are connected, and there is one step connecting unit A to unit C. Small-world structure is present if the small-world coefficient (S) is greater than 1 (S>1) (Watts and Strogatz, 1998; Humphries and Gurney, 2008).

5.4 Results

5.4.1 Similarity analysis

Song types (Teal or Orange) were grouped onto the two separate major dendrogram branches, and were clearly distinguished from one another based on their respective unit sequences (Fig. 5.2). Within each major branch (song type), song cycle unit sequences were not further separated based on population (Fig. 5.3). Instead, the song cycles from each song type were mixed on most major branches regardless of the population of origin. This verified the existence of two distinct and unrelated song types based on fine-scale unit sequences as well as the established similarity in broad scale theme sequences (Garland *et al.*, 2011). The Teal song repertoire shared 75% of unit types between populations, while the Orange song repertoire shared 68% of unit types between populations (Table 5.3).

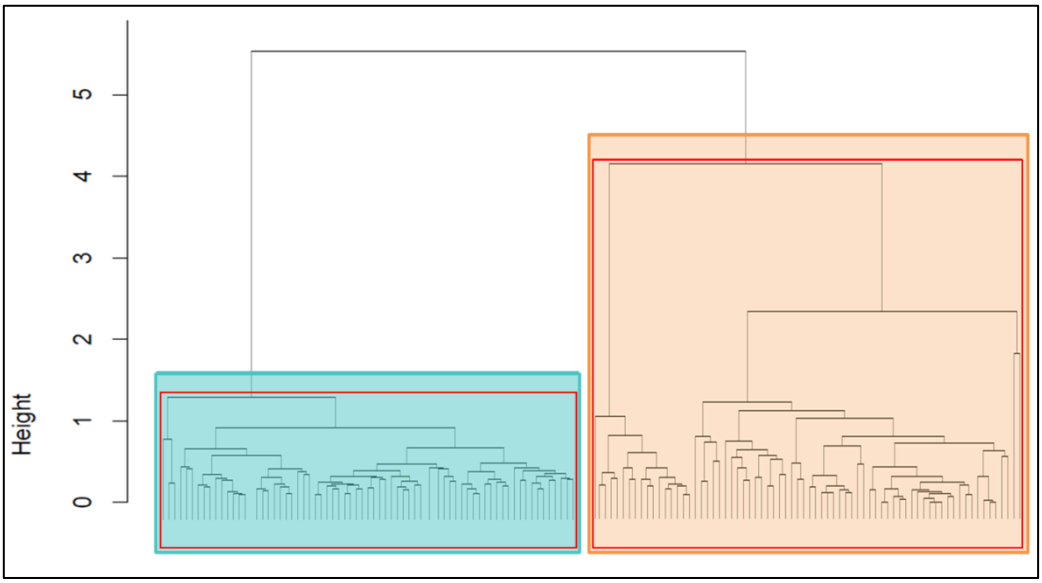
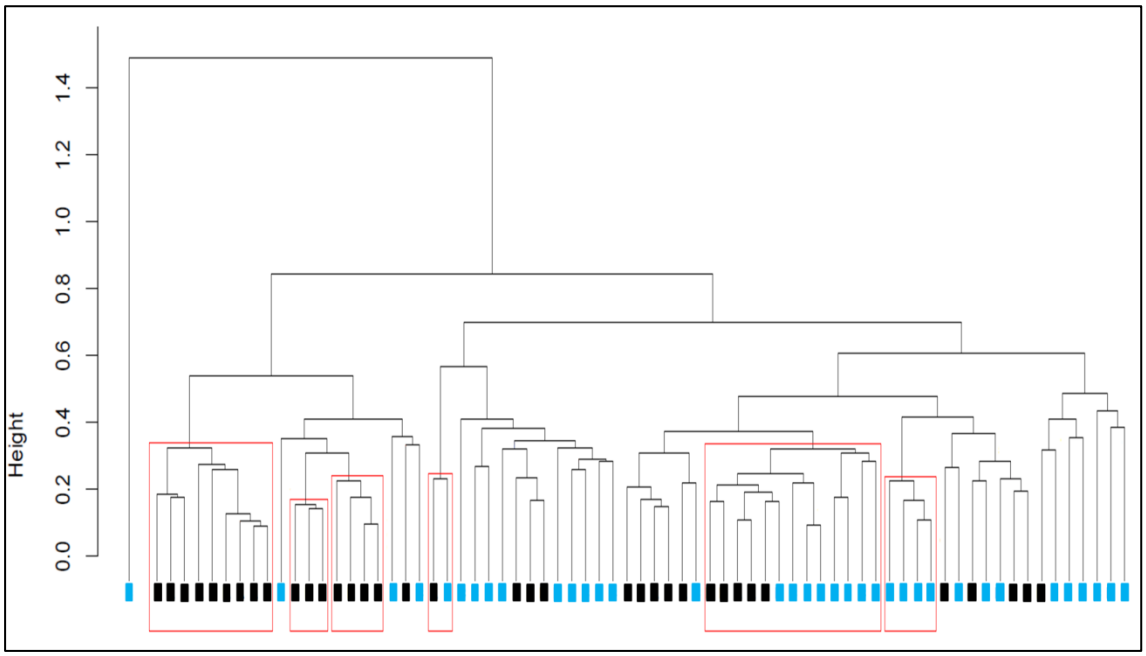


Figure 5.2 Similarity analysis of set median song cycles across populations. Dendrograms show bootstrapped (1000 times) average linkage hierarchical cluster analysis for similarity matrices of set median unit sequences for every song cycle from both populations (N=144, CCC=0.97). The degree of similarity between any two branches is reflected in their height. Branches at similar heights indicate their degree of similarity based on average distance between them as calculated by the LSI. Red boxes indicate that the branches within are a true representation of the data with 95% confidence, based on multi-scale bootstrap resampling. Branch colours indicate the song types (Teal or Orange) that each branch represents. Terminal nodes represent individual song cycles

a)



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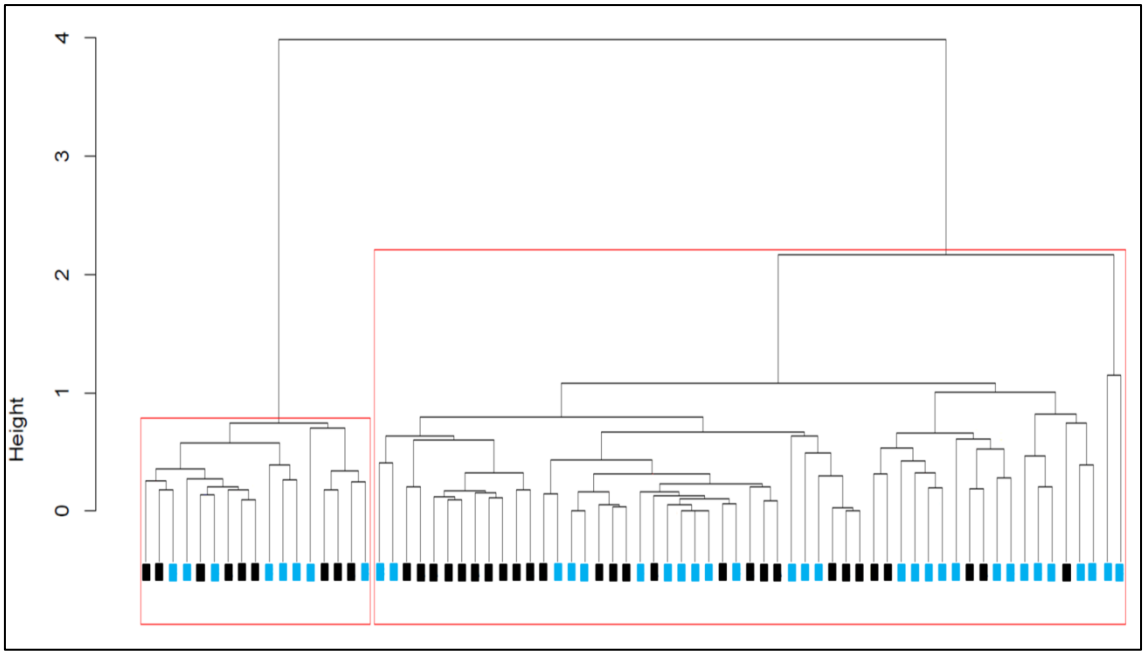

Figure 5.3 Dendrograms showing similarity within each song type between the east Australian and New Caledonian populations (inter-population song similarity). Bootstrapped (1000 times) average linkage hierarchical cluster analysis was based on similarity matrices of set median unit sequences of every song cycle for the a) Teal song type (N=72, CCC=0.74) and b) Orange song type (N=72, CCC=0.97), regardless of the population. Terminal nodes represent individual song cycles (East Australia=black and New Caledonia=blue). The degree of similarity between any two branches is reflected in their height. Branches at similar heights indicate their degree of similarity based on average distance between them as calculated by the LSI. Red boxes indicate that the branches within are a true representation of the data with 95% confidence, based on multi-scale bootstrap resampling. Multiple linkages were tested for the Teal song type and none met the CCC=0.8 threshold. Average linkage provided the best representation.

Table 5.3 Repertoire and usage (counts) for each song type in each population. Counts are the number of times a unit was recorded within the song's full sequence of units. Repertoire is ordered from the most frequently used to least frequently used. The top five most commonly used units have the percentage of occurrence in parentheses (i.e., 10% means that the particular unit type made up 10% of all units used in song sequences for that respective song type). For each repertoire, darkened units are unique to that population's repertoire.

Teal Song Type				Orange Song Type			
East Australia 2013		New Caledonia 2014		East Australia 2014		New Caledonia 2015	
Unit	Count	Unit	Count	Unit	Count	Unit	Count
58	937 (14%)	**58**	634 (15%)	**126**	1486 (20%)	**69**	1143 (16%)
67	868 (13%)	**67**	503 (12%)	**69**	1112 (15%)	**133**	1013 (14%)
59	723 (11%)	**45**	379 (9%)	**34**	692 (9%)	**14**	903 (12%)
69	697 (11%)	**59**	351 (8%)	**125**	628 (9%)	**125**	798 (11%)
45	495 (8%)	**6**	279 (7%)	**133**	562 (8%)	**126**	734 (10%)
63	471	**60**	249	**20**	476	**75**	547
6	427	**69**	237	**75**	447	**20**	442
38	401	**53**	219	**127**	317	**142**	215
60	324	**52**	140	**14**	304	**50**	201
53	217	**63**	116	**48**	224	**24**	187
46	132	**38**	109	**144**	176	**34**	146
42	88	**42**	94	**134**	172	**134**	146
52	79	**2**	64	**138**	157	**144**	131
83	76	**3**	61	**74**	74	**85**	76
3	63	**11**	53	**24**	67	**54**	70
27	62	**16**	53	**10**	66	**48**	60
78	52	**83**	52	**142**	52	**35**	42
22	42	**78**	44	**84**	36	**138**	42
16	38	**46**	41	**85**	19	**10**	22
2	37	**12**	35	**25**	18	**100**	22
12	32	**18**	16	**100**	17	**84**	11
39	31	**1**	14	**54**	12	**74**	9
55	26	**20**	14	**45**	10	**45**	8
11	19	**27**	7	**35**	8	**25**	3
21	16	**22**	6	**50**	8	**127**	3
18	9	**55**	4	**90**	6	**17**	1
1	6	**19**	3	**53**	4	**53**	1
19	6	**23**	3	**17**	1	**90**	1
23	6	**21**	2	**118**	97	**111**	174
40	4	**40**	2	**19**	19	**132**	43
13	3	**13**	1	**79**	19	**123**	32
31	3	**31**	1	**89**	12	**83**	21
20	2	**39**	1	**37**	9	**70**	18
44	64	**57**	267	**28**	6	**55**	11
29	18	**70**	111	**46**	4	**109**	7
17	8	**82**	34	**29**	3	**82**	5
48	8	**35**	9	**44**	3	**57**	4
41	6	**9**	3	**38**	2	**104**	3

32	4	**30**	1	**5**	1	**117**	1
49	4	**64**	1	**40**	1		
108	4			**60**	1		
28	3						
50	3						
56	3						
101	2						
105	2						
4	1						
5	1						
71	1						

Equivalent themes from each population always clustered together on the same branch, with the unit sequences of each theme having an average similarity of at least 80% between populations (Fig. 5.4). This verified that themes largely retained their unit sequence patterns across populations in a recognisable way (Table 5.1). Dendrograms for both song types had a CCC score of > 0.9 (Teal: CCC=0.97, Orange: CCC=0.99), indicating a good representation of the associations in the data.

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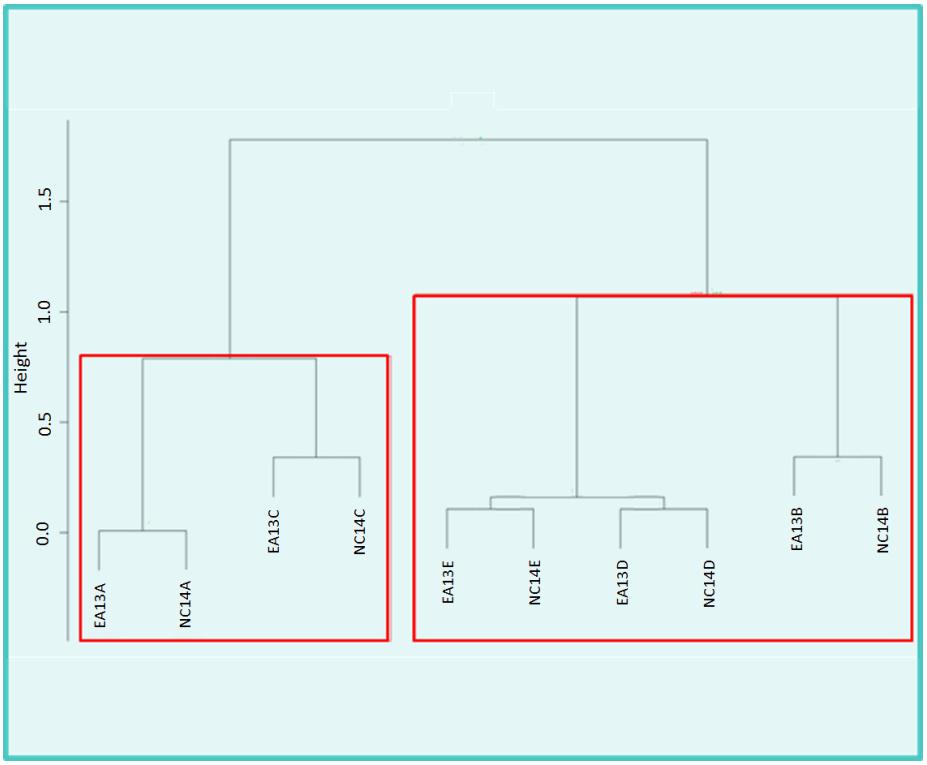

b)

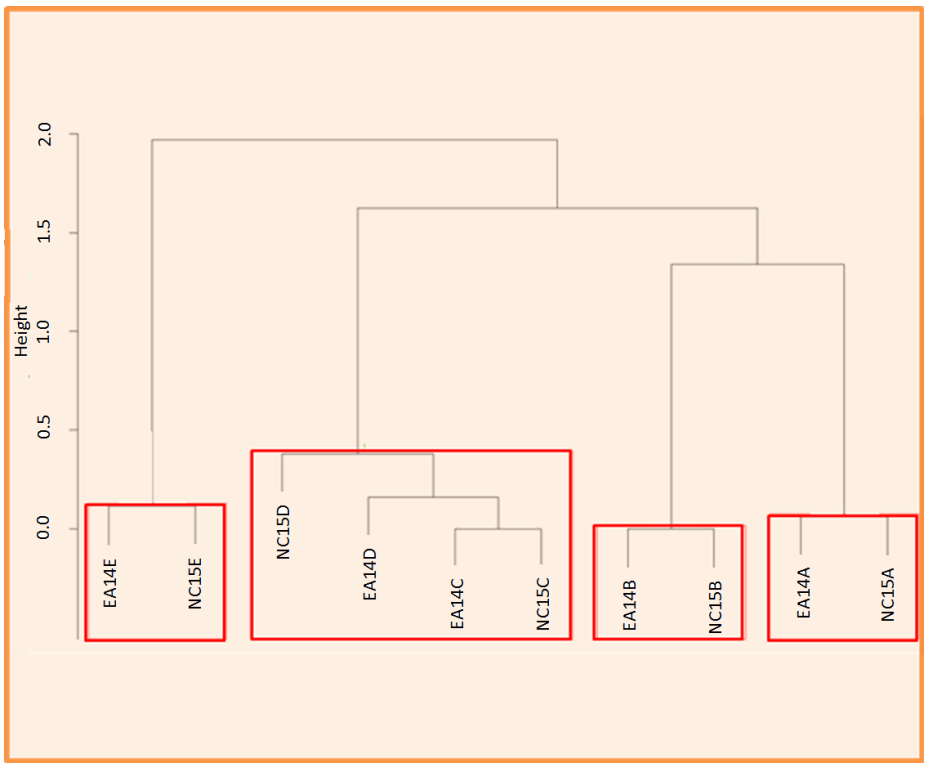

Figure 5.4 Dendrograms showing similarity in song structure across populations for each theme (outlined in Table 5.1) for a) the Teal song type (CCC=0.97) and b) the Orange song type (CCC=0.99). Bootstrapped (1000 times) average linkage hierarchical cluster analysis was used based on similarity matrices of median unit sequences. The height (y-axis) of two branches reflects the LSI distance between them. Red boxes indicate that the branches within have an approximately unbiased (AU) p-value greater than 95% and are strongly supported by the data based on multi-scale bootstrap resampling. Themes are labelled by population (EA or NC), year (2013- 2015), and theme letter (A-E).

5.4.2 Complexity

Complexity scores served as a reliable indicator of complexity within a song arrangement (Boogert et al. 2008; Templeton et al. 2014; Chapter 3). The positive correlation between variables meant that variables could be combined and reduced to a single principal component which served as a representative measure of complexity. The three song-level variables (number of units per song cycle, number of unit types per song cycle, duration of each song cycle) were positively correlated ($p<0.05$ between all variables), and the unrotated PCA for song level complexity extracted a single principal component that explained 80% of the variance with an eigenvalue of 2.4. The three theme-level variables (number of themes per song cycle, mean phrase duration per song cycle, mean individual theme complexity score per song cycle) were all positively correlated ($p<0.05$ for all) and the PCA for theme-level complexity extracted a single principal component which explained 77% of the variance with an eigenvalue of 2.3. Song-level complexity scores were lower in New Caledonia for both song types compared to east Australia (Fig. 5.5). New Caledonia's songs were shorter in duration, and contained both fewer units and fewer unit types.

Further examination of the song sequences revealed that east Australia had significantly more phrase repetitions per song cycle than New Caledonia in both song types (Mann-Whitney/Wilcoxon test: Teal song type: W=97, p<0.01, Orange song type: W= 475, p=0.05). Unlike song-level scores, theme-level scores were higher in New Caledonia for both song types. New Caledonia's songs had a higher number of themes present per song cycle, and those themes each tended to be longer and contained a higher number of units and unit types (Fig. 5.5). Population differences were more substantial for the Teal song type (in both the song and theme-level measures) than for the Orange song type.

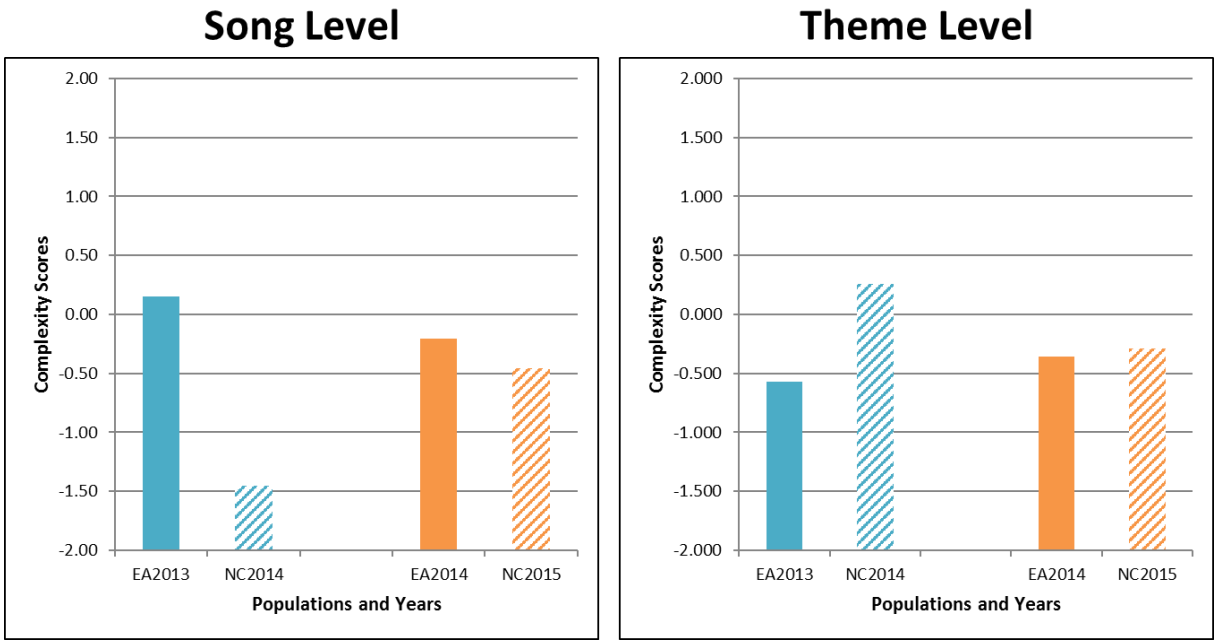

Figure 5.5 Complexity scores were calculated for the a) Teal song type and b) Orange song type. Scores were calculated for each population using variables at the song level only and the theme level only

For individual theme complexity scores, the first principal component score from the unrotated PCA extracted one principal component which explained 67% of the variance with an eigenvalue of 2.0. There was no significant difference in theme complexity scores between populations for either song type (Mann-Whitney/Wilcoxon, Teal: W=8, p=0.40 and Orange: W=13, p=0.98). Individual theme scores were higher in New Caledonia for all but one theme (Fig. 5.6). For the majority of themes, the New Caledonian version contained a higher number of units, more unit types, and longer durations compared to east Australia. For example, east Australia's version of Teal theme C had an average of 10.1 units per phrase, 3.8 unit types, and an average length of 16.1 seconds. New Caledonia's version of Teal theme C had an average of 11.6 units per phrase, 5.0

unit types, and an average length of 17.3 seconds. Differences primarily occurred due to substitution of acoustically similar units, and an increase in repetitions of common patterns which increased both duration and the number of units per phrase (see Chapter 4 for details on common fine-scale patterns). For example, the phrase length and number of units per phrase in Teal theme C increased due to the repetition of the alternating "69, 67" pattern (Table 5.1) one or two times more in New Caledonia compared to east Australia. Unit 69 was a flat, low frequency, short duration moan while unit 67 was a low frequency, short duration "bark" which increases in frequency. The number of unit types increased in New Caledonian Teal theme C as unit type 69 was occasionally substituted with the acoustically similar unit type 57 (both were flat, low frequency, short duration moans). Similar kinds of variations were found to drive changes in complexity for most of the individual theme comparisons.

Theme E from the Orange song type was the only individual theme that was more complex in the east Australian version of the song. This was due to differences in the number of units present in the theme, as the east Australian version contained a higher number of units per phrase repetition. These units were low frequency, short duration broadband calls known as "grunts", which commonly occur in bouts or series of repetitions (Chapter 4). Therefore, the New Caledonia version of Theme E had fewer repetitions of the same units compared to east Australia, and those repetitions were slower with longer inter-unit intervals.

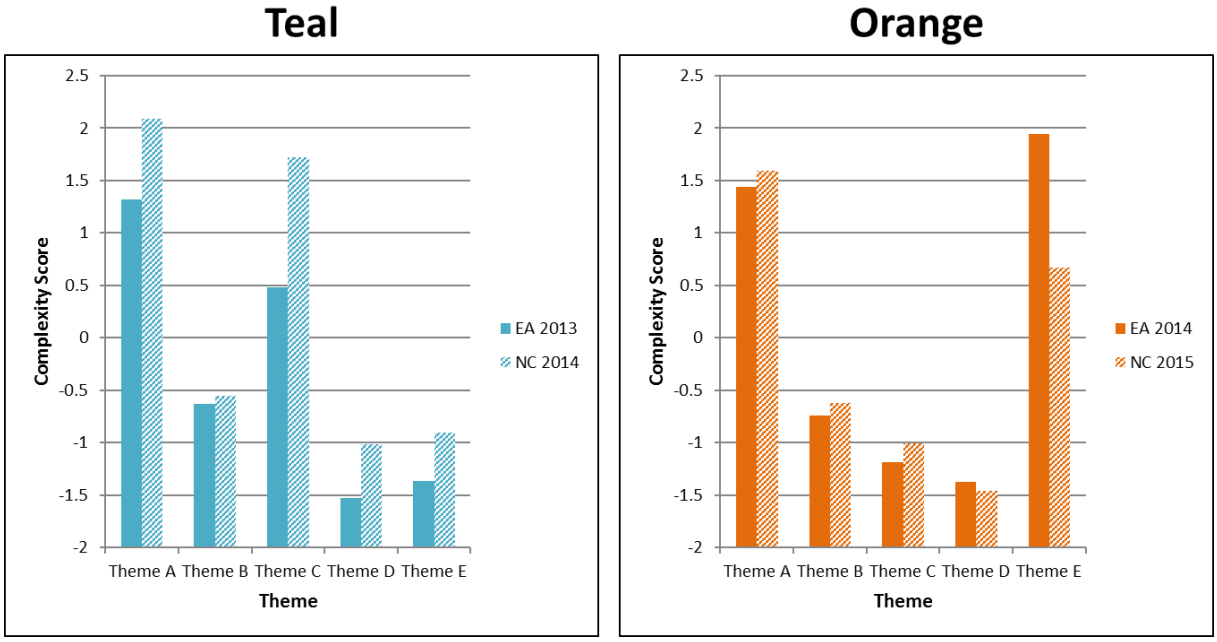

Figure 5.6 Complexity scores were calculated for every theme in the a) Teal song type and b) Orange song type. Scores were calculated for the song types as they appeared in each population. Note that there are no shared themes between the Teal and Orange song types.

5.4.3 Information entropy estimates

Second order entropy estimates convey how predictably sequences were arranged. Entropy estimates for theme sequences did not change across populations for either song type (Fig. 5.7), though theme sequences were more stable for the Teal song than for the Orange song. Theme sequences were therefore equally predicable in their arrangement across populations. Unit sequence entropy was lower in New Caledonia for the Teal song type, but showed no difference across populations for the Orange song type (Fig. 5.7). The lower entropy in New Caledonia for the Teal song type indicates that units were less predictable in the east Australian version. Similar to the decreased song-level complexity seen in the New Caledonia song, it is likely that east Australia's unit sequences were less predictable because the songs were longer due to more phrase repetitions, providing more opportunity for unit sequence variation.

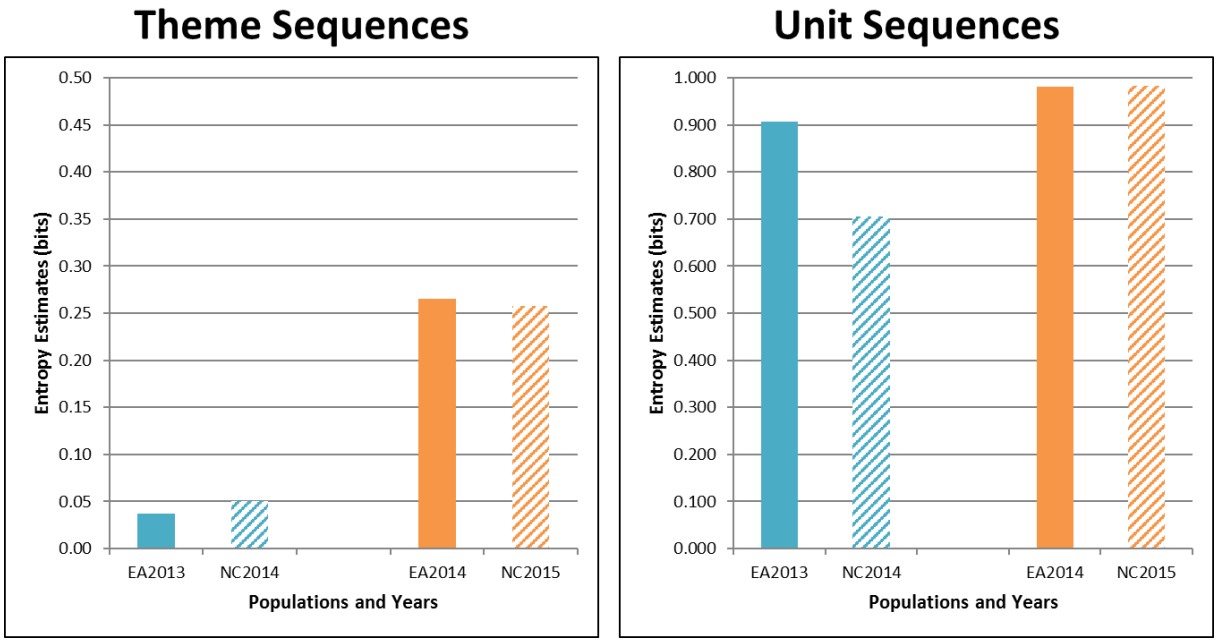

Figure 5.7 Second order entropy estimates (bits) were calculated for theme sequences and unit sequences for each population, year, and song type. Theme sequences have a scale of 0.0-0.5 bits, unit sequences have a scale of 0.0 to 1.0 bits

5.4.4 Network analysis

Four separate directed network models were created, one for each song type (Teal or Orange) in each population (east Australia or New Caledonia). Network models were based on the 36 complete song cycles for each respective dataset (Appendix 3). There was no change in small-world coefficients for each song type between populations (see Table 5.4 for a full summary of network features). Fine-scale variations in the networks showed small, but negligible differences in which units were connected and how often. Therefore, the overall degree of connectivity between units (i.e. which units were adjacent in the display and how often) did not change during song transmission of either song type.

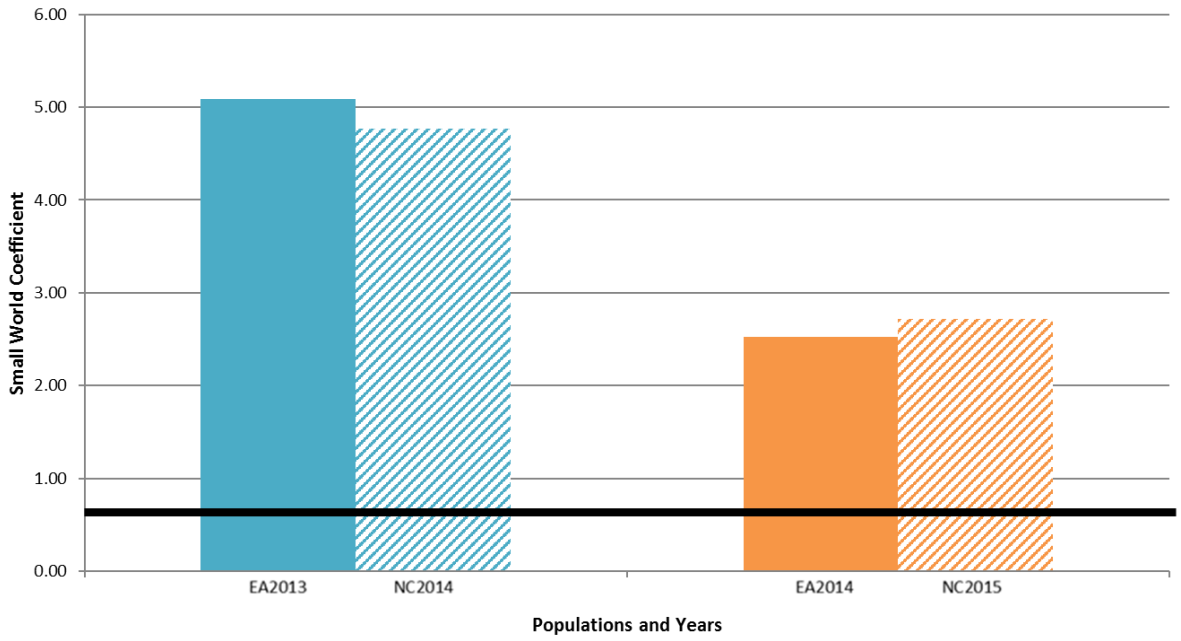

Figure 5.8 Small-world coefficients (S) for the network models of the Teal and Orange song types in each population (N=36 song cycles per population/year). The threshold for small-world topography (S=1.0) is marked.

Table 5.4 Network features for each population/year. Features include the small-world coefficient (S), path length (L), clustering coefficient (C), unit repertoire size, and the number of small-world themes present

Song Type	Population	Year	S	L	C	Repertoire	SW Themes
Teal	East Australia	2013	5.1	2.0	0.7	48	4
Teal	New Caledonia	2014	4.8	2.1	0.7	40	4
Orange	East Australia	2014	2.5	2.0	0.5	41	6
Orange	New Caledonia	2015	2.7	1.9	0.6	39	6

5.5 Discussion

Singers in New Caledonia appear capable of learning the fine-scale unit arrangements of each song type with a high degree of fidelity. Unit sequences had high enough similarity that song types were clearly distinguished regardless of which population the song came from (Fig. 5.2). This demonstrates that songs in east Australia and New Caledonia are highly similar at a fine-scale level as well as at the broad-scale level of theme sequences (Garland *et al.*, 2011). Unit sequence similarity was strong enough that analyses could not further distinguish which population a recorded song came from (Fig. 5.3). Units that were unique to a single population (25% of the Teal song repertoire, 32% of the Orange song repertoire) actually occurred within song sequences less than 10% of the time, showing that fine-scale differences were limited (Table 5.3). Further supporting this inter-population similarity was the retention of comparable degrees of small-world structure (Fig. 5.8). As expected, this indicates that the degree of connectivity (i.e., which units are adjacent to each other and how often) did not appreciably change during inter-population transmission. Ultimately the lack of differences in unit arrangements demonstrates that there is no clearly distinct "east Australian" or "New Caledonian" version of each song type. New Caledonian singers therefore learn song patterns from east Australia as accurately as individuals within east Australia learn from each other. Stability in the underlying network structure may enable song learning across populations, as suggested by their role within a single population (Chapter 4).

Among shared unit types, units with similar acoustic features were typically used in similar ways by each population. For example, unit types 14 and 34 occurred within Orange theme A for both populations. New Caledonian whales often sang unit type 14, while east Australian singers tended to use unit type 34 (Table 5.1). Both units have very similar acoustic features: they are long, descending, modulated tonal calls with a similar frequency range and contour shape. This example and similar kinds of changes between the New Caledonian and east Australian song in other themes suggests that many of the small, fine-scale population differences are substitutions of similar unit types that may be copy error or unit types that whales use interchangeably. However, similarity analyses indicate that these differences are not substantial enough to clearly distinguish one population from the other (Fig. 5.3). New Caledonian singers learn unit sequences with as much fidelity as possible, using unit types that are the same or highly similar in their characteristics to those sung by east Australian singers.

Shared unit types covered the spectrum of acoustic features such as frequency, duration, and contour shape. Of note was the retention of sequences containing high frequency unit types (i.e.

"whistles" or "squeaks") during song transmission. Typically, high frequency signals do not propagate as far as low frequency signals and thus can be lost over distance (Winn and Winn, 1978; Girola *et al.*, In Review). Recent work by Girola *et al.* (In Review) also found that source levels in humpback whale song decrease with increasing frequency. The results found here suggest that the mechanism of song exchange between the populations allows for sufficient acoustic contact and high fidelity copying as all sequences can be learned (including those containing high frequency units). Such acoustic contact could occur on the Antarctic feeding grounds (Garland *et al.*, 2013a) or through the New Zealand migration corridor shared by both populations (Constantine *et al.*, 2007; Steel *et al.*, 2008). The limited individual exchange documented thus far between east Australia and New Caledonia (Garrigue *et al.*, 2011b) suggests the movement of individuals either within or between seasons is less likely as a mechanism for song transmission than feeding ground and migratory exchange but cannot be ruled out.

Individual themes were learned with particularly high accuracy. Equivalent themes within each song type maintained at least 80% similarity across populations. Furthermore, contrary to our hypothesis, complexity in each individual theme either remained equal or increased when it was learned by New Caledonia. Increases in complexity were driven by increased repetitions of units or short patterns within the theme, as well as substitutions of separate but acoustically similar unit types. This suggests that song transmission between populations does not require individuals to simplify the novel fine-scale patterns of each theme in order to facilitate learning. The Teal and Orange song types were considered average complexity songs, ranked 8th and 9th respectively among the 13 song types analysed in east Australia (Chapter 3). If complexity is indeed an indication of learning capacity, as suggested in both songbirds (Catchpole, 1996; Nowicki *et al.*, 2000; Boogert *et al.*, 2008) and humpback whales (Chapter 3), then maintaining complexity in a song arrangement is arguably more important in a breeding ground such as New Caledonia compared to the east Australian migratory corridor. This supports the hypothesis proposed by Garland *et al.* (2017a) that themes are the fundamental "building blocks" of song learning.

Higher theme-level complexity in New Caledonia was driven by more themes in each song cycle, longer phrase durations, and higher individual theme complexity, while small decreases in each song cycle's duration, number of units, and number of unit types resulted in slightly lower song-level complexity. Contrary to this, complexity in east Australian songs had parallel trends at both the song and theme levels (Chapter 3). This could be partially explained by the significantly higher number of phrase repetitions found in east Australia. A higher number of phrase repetitions

impacts song-level complexity because it increases the number of units and unit types present in the entire song cycle, as well as making the entire display longer. Phrase repetitions are a variable aspect of the song (Cholewiak, 2008) which may change based on social context (Smith, 2009). The differences in phrase repetitions and by extension, the lower song-level complexity of New Caledonia's version of each song type, suggest that the migration route of east Australia and the breeding ground of New Caledonia are different social contexts.

Variations and novelty in song patterns are thought to be driven by the changes of individual singers (Noad, 2002), which are then learned by all singers through song conformity. The much larger population in east Australia (Garrigue *et al.*, 2001; Noad *et al.*, 2006) has more singers and therefore may provide more sources for novelty for any given singer (Noad, 2002). While these population level differences may account for limited variability, high song similarity and stable entropy estimates suggest that they do not result in a meaningful distinction between populations.

Each theme is highly similar to repetitions of itself (Fig. 5.4), but there are multiple phrase repetitions of each theme. Each of these repetitions has small variations which do not have a large impact on the similarity of each theme because phrase only contain a small number of units. However, the small variations of each repetition add up to much bigger differences over the course of an entire song cycle which contains hundreds of units. As a result, the unit sequences of each theme retained higher similarity amongst themselves (~80%) during song transmission than the much longer unit sequences of song cycles as a whole (~60%). Unit sequence variations throughout a song cycle occur in both populations, explaining why they were not clearly distinct from one another (Fig. 5.3). This suggests that there are equal amounts of fine scale variability in song learning both within and between populations.

The consistent, directional song transmission between east Australia and New Caledonia provides a unique opportunity to examine the product of song learning at an inter-population level. These populations are part of a broader case of horizontal cultural transmission on a large scale, the only example that has been documented in a non-human species (Garland *et al.*, 2011). We have quantitatively shown consistency in fine-scale structural features across populations to complement broad-scale analyses (Garland *et al.*, 2011; Garland *et al.*, 2015). Complexity within these song types did not decrease during transmission, suggesting that constraints on song learning may not impact inter-population transmission. Although learning cannot be directly observed, song patterns provide indirect evidence regarding the learning mechanisms in use. The results found here suggest

a learning mechanism that allows for high fidelity learning of complex song arrangements between populations, such as transmission on shared feeding grounds or migration routes. Given that cultural exchange between populations has not been documented in any other species apart from humans, humpback whale song provides a model by which the evolution of cultural transmission in both animals and humans can be further understood.

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CHAPTER 6 General discussion and conclusions

6.1 Cultural traditions in animals

Humpback whales have cultural traits in multiple aspects of their ecology (Whitehead and Rendell, 2014). Strong maternally directed site fidelity to both breeding and feeding grounds results in limited exposure to other populations (Payne and Payne, 1985; Baker, 1986; Calambokidis *et al.*, 2001). Such segregation from external influences can lead to population-specific cultural trends. In addition to their song, a novel foraging strategy has also been documented spreading culturally through a population in the North Atlantic (Allen *et al.*, 2013). This was demonstrated by tracking the cultural trait from its appearance in a single individual through 27 consecutive years. Transmission of the trait followed the social network of the individuals, spreading between associated individuals that spent time together.

Unlike the foraging cultural trait, the learning mechanisms of song are indirectly studied by examining the result of the transmission: the song's pattern. If the song patterns of individual singers could be recorded in multiple years, as well as the social network of the population in those years, then the transmission mechanism could be examined more directly. In the east Australian population, this would be impossible due to its size (> 25,000; Noad *et al.*, 2016). However, the reliable directionality of the cultural transmission in the South Pacific means that song learning and social networks could be assessed in a much smaller populations like New Caledonia.

The presence of multiple cultural traits in humpback whale ecology demonstrates that multiple cultural traditions are possible in a non-primate species (Garland *et al.*, 2011; Allen *et al.*, 2013; Whitehead and Rendell, 2014). Previously, the only documented case in a non-human species was a suite of cultural traits involving tool use in populations of chimpanzee (*Pan troglodytes*) throughout Africa (Whiten *et al.*, 1999). Further study of cultural traits in humpback whales, as well as other cetacean species, will expand the body of knowledge on how cultural traditions have evolved in multiple animal species and provide an understand of their evolution in humans.

6.2 Summary of findings and significance

The main aim of this thesis was to investigate the fine-scale structural patterns and features of humpback whale song to further our understanding of vocal learning during broad-scale cultural transmission. Unlike bird song studies which have explored the fine-scale syntax and complexity of

vocal learning displays (Berwick *et al.*, 2011), previous humpback whale song studies have focused either on broad-scale features such as theme sequences (Chu and Harcourt, 1986; Eriksen *et al.*, 2005; Garland *et al.*, 2011; Murray *et al.*, 2012), qualitative study of song change over a long period (Payne and Payne, 1985), or brief snapshots of song over a few years (Helweg *et al.*, 1998; Noad *et al.*, 2000; Cerchio *et al.*, 2001; Arraut and Vielliard, 2004; Darling *et al.*, 2014; Murray, 2015). This thesis quantified fine-scale song change at the unit level in humpback whale songs over 13 consecutive years in a single population, as well as between two neighbouring populations over three consecutive years.

Several analytical tools were developed or modified to quantify fine-scale humpback whale song structure. A representative acoustic dictionary for the song repertoire was developed (Chapter 2) and applied to all subsequent chapters (Chapters 3-5), allowing for the quantified, robust, and repeatable classification of units and song transcription (Allen *et al.*, 2017). Chapter 3 modified a method originally used to quantify complexity for birdsong by Boogert *et al.* (2008) and Templeton *et al.* (2014). These 'complexity scores' could not be directly applied to humpback whales due to the multi-level hierarchy of their song compared to the linear structure of birdsong. Additional variables were incorporated to reflect the unique 'theme' level of humpback whale song structure. Metrics to quantify underlying structural features were also applied, including predictability of arrangements through second-order entropy (Chapter 3, Chapter 5), patterns in unit sequences through network analysis (Chapter 4), and Levenshtein distance analysis (Chapter 5). Quantitative measures of these fine-scale features are important for objective and direct comparisons of humpback whale songs across song types (Chapters 3-4) and populations (Chapter 5)

Comparisons of both progressive evolutions and radical revolutions highlighted which song features were present during both types of change and which features were flexible (Chapter 3-5). Certain underlying syntactic song features (specifically small-world network structure, connectivity of unit types, and unit usage) were consistently present through time within the east Australian population (Chapter 4). The degree of small-world structure (reflected by the small-world coefficient S; Humphries and Gurney, 2008) fluctuated due to a number of factors which influence how units are connected within sequential patterns. For example, high S-value can result from a song type with many units that were all highly connected (i.e. units that often occur adjacent to one another in a sequence) or from a particular unit type that was frequently used across several themes within the song. Despite these changing values due to a combination of influences, small world networking was apparent in every year in both populations studied (Chapter 4).

In contrast to the consistent presence of network structure, song complexity fluctuated in a clear pattern over time both within and between populations (Chapters 3, 5). This fluctuating pattern reflected the two types of change to the east Australian song: complexity increased with evolutionary changes while it decreased with cultural revolution events where songs were introduced, most probably from the west Australian population (Chapter 3). Each theme retained or increased its individual complexity during inter-population song transmission, suggesting that a more complex arrangement is not more difficult to learn across populations (Chapter 5). Song learning therefore occurs by combining these fine-scale changes in complexity (Chapter 3) with underlying structures that facilitate learning (Chapter 4) and high fidelity song matching (Chapter 5). This results in the dynamic cultural transmission of humpback whale songs.

6.3 Fine-scale song evolution and revolution in a single population

Over the course of the 13-year study, songs underwent both evolutionary and revolutionary changes that were quantified at the unit level. These 13 song types were grouped into eight separate song lineages: Blue (2002), Red (2003-2005), Yellow (2006), Green (2007-2008), Purple (2009-2010), Brown (2011-2012), Teal (2013), and Orange (2014). Evolutions and revolutions (as well as colour identifiers) corresponded with those identified and described by Garland et al. (2011) for 1998-2008 and 2002-2010 in Rekdahl et al. (2012). Three new lineages were additionally identified here in 2011-2012 (Brown), 2013 (Teal), and 2014 (Orange) (Chapter 3). The Red, Green, Purple, and Brown song lineages underwent progressive, evolutionary changes over consecutive years. Each of these lineages contained two related song types, i.e., songs that shared at least one theme. Song types were assigned a "dark" and a "light" shade except for the Red lineage, which evolved over three years and were thus identified by three shades: dark, normal, and light. Here, related themes which evolved between years were identified quantitatively through an LSI analysis of unit sequences which was weighted to reflect acoustic similarity between units (Chapter 2, Garland *et al*., 2017, Allen *et al.*, 2017).

Related themes themselves tended to evolve through additions of new unit types and increased repetitions of current units (Chapter 3). As the songs evolved from one year to the next in our study, these changes resulted in increased levels of complexity within themes that are shared between evolving song types (Chapter 3). Other themes did not evolve, but instead were replaced with new, unrelated themes as observed in multiple populations around the world (Payne and Payne, 1985; Cerchio *et al.*, 2001; Garland *et al.*, 2011; Darling *et al.*, 2014). Similar to the increased complexity in evolving themes, these new themes were more complex than the ones that

were deleted through higher number of units, number of unit types, and longer phrase durations (Chapter 3). Complexity also increased at the song level during evolutions. Songs became longer, the number of unit types used increased (within both shared and unique themes), and the number of different themes sung per song cycle increased. Such consistent increases were not reflected in the network structure of the evolving songs. Instead, clear small-world structure (S>1; Humphries and Gurney, 2008) where units are clustered into highly connected groups (Watts and Strogatz, 1998) was always present to varying degrees. The degree of small-world structure was not correlated with the increasing complexity of the song arrangements. Underlying network structure was therefore unrelated to the complexity of the song's fine-scale arrangement, suggesting that degree of complexity is not a fixed featured of song the way network structure is.

Revolution events have been a consistent cultural phenomenon in the South Pacific over almost 20 consecutive years (Noad *et al.*, 2000, Garland *et al.*, 2011, Rekdahl *et al.*, 2012, Garland *et al.*, 2013, Chapter 3). In the years covered in this thesis (2002 – 2014), cultural revolution events, when one song lineage was replaced with another, occurred in seven instances: Blue to Red, Red to Yellow, Yellow to Green, Green to Purple, Purple to Brown, Brown to Teal, and Teal to Orange. Revolutions were first recorded in east Australia between 1996 and 1997 (Noad *et al.*, 2000), with confirmation that documented revolutions through 2010 originated from the west Australian population (Rekdahl, 2012). These song types did not contain any shared themes and thus had 0% similarity based on the weighted LSI analysis (Chapter 2, Allen *et al.*, 2017). New, revolutionary song types had a simpler structure and arrangement than the songs that they replaced in every instance: they contained fewer units and unit types, fewer themes that had shorter phrase durations, and shorter overall song durations (Chapter 3). As with evolving song lineages, the consistent decrease in complexity seen during cultural revolution events did not occur in the song network structures (Chapter 4), further confirming that complexity and network structure were unrelated.

Continuous changes mean that each song type contained different numbers and types of units. Changes included additions of novel material through new unit types or entirely new themes, resulting in continuous changes to song complexity. Song conformity emphasizes learning ability because every male must adopt to these changes in the song pattern even as the song increases in complexity (Noad, 2002; Logue and Forstmeier, 2008). However, these changes to complexity were not reflected in second-order information entropy (Chapter 3), suggesting that specific unit arrangements are a flexible aspect of the song and unlikely to contain or be part of any information

the singers may be trying to convey. This means that while the display's pattern may change, its function and general message do not.

6.4 Structural features aid in song learning

The degree of predictably in a song arrangement, indicated by second order entropy, remains relatively stable both within a population (Chapter 3: 0.8 to 1.8 bits for unit sequences, 0 to 0.6 bits for theme sequences) and during inter-population transmission (Chapter 5: 0.7 to 1.0 bits for unit sequences, 0 to 0.3 bits for theme sequences). Two previous studies have assessed entropy in humpback whale song, one examining two consecutive years of song in Hawaii (Suzuki *et al.*, 2006) and one examining the 2003 song from the east Australian population (Miksis-Olds *et al.*, 2008). Results using the Markov first-order model, equivalent to the methods used here, found similar average estimates in both studies (1.0 bits for Suzuki *et al.*, 2006 and 0.97 bits for Miksis-Olds *et al.*, 2008) which were also similar to the results found here (average of 1.2 bits, Chapter 3; average of 0.9, Chapter 5). Despite methodological differences in these studies (both Suzuki and Miksis-Olds assessed song sessions rather than the discreet song cycles used here), all three still demonstrate that songs contain predictable fine-scale arrangements even when those patterns evolve or get entirely replaced. These studies quantitatively corroborate the established predictability of a repetitive hierarchical song structure (Payne and McVay, 1971). Predictable song arrangements are likely to facilitate learning for a constantly evolving display.

Small-world structures mean that every song type had certain units with a tendency to occur adjacent to one another within song sequences (Chapter 4). Deterministic transitions between these adjacent units restrict which units follow one another (Sasahara *et al.*, 2012), encouraging the fine-scale stereotypy and predictability of humpback whale song arrangements. These deterministic patterns were the most frequently occurring transitions; doublet, triplet, and alternating repetitions were common across a range of unit types, while long repetitive bouts were common for short, low frequency units (Chapter 4). These patterns were always present despite extreme differences in the themes and unit sequences of separate song lineages (Chapter 4). Such recurring and repetitive patterns are hypothesised to make song learning easier because the patterns are akin to 'rhyming' (Guinee and Payne, 1988).

Such consistency in the presence of these network features over an extended period of time across multiple song types (Chapter 4, Chapter 5) supports aspects of the 'innate template' hypothesis (Cerchio *et al.*, 2001). This hypothesis suggests that all songs follow a template of basic

structural rules that determine how the song is arranged or how it changes. Network analysis over 13 consecutive years suggests that the template is based on underlying features like small-world structure and deterministic transitions patterns which support stability (Chapter 4). An innate template based on these network features would allow the innate template hypothesis to coexist with the wide variety of unit types and arrangements seen in song types within and across multiple populations. Similar innate auditory templates are used during the learning period of many songbirds (Marler and Sherman, 1983; Konishi, 1985), several of which have similar network structure to that demonstrated here in humpback whale song (Sasahara *et al.*, 2012; Deslandes *et al.*, 2014; Weiss *et al.*, 2014; Taylor and Cody, 2015; Cody *et al.*, 2016). Although such innate templates have been suggested for humpback whale song in previous studies (Cerchio *et al.*, 2001; Garland *et al.*, 2011), the research here provides strong quantitative evidence of such a template based on newly identified fine-scale network features of song structure which complement the well-established hierarchical structure of the song (Payne and McVay, 1971).

Singers from New Caledonia learn and retain song arrangements from east Australia with a high degree of fidelity (Chapter 5). Such fidelity in learning suggests a means of acoustic contact that allows for the detailed learning observed (Chapter 5). Each separate theme was repeated multiple times with small variations, which added up to much more variations over the course of entire song cycles. This resulted in song cycles as a whole contains more variability than each of the themes individually, which were each learned with accuracy (~80% similarity, Chapter 5). Unit sequence variability therefore seems to result from differences in these phrase repetitions. The variability between the two populations was similar to that seen within a population, indicating that this kind of unit sequence variability is probably normal in song learning among whales regardless of whether in the same or different populations. Most inter-population differences involved acoustically similar units, suggesting copy-error rather than 'intentional' population-specific changes (Chapter 5). Overall, learning each of the themes accurately was more common than maintaining high similarity across the entire song cycles. This supports the hypothesis that themes are the "building blocks" of song learning as suggested by Noad (2002) and Garland *et al.* (2017a).

6.5 Vocal learning and cultural processes

Humpback whale song, complex birdsongs, and human language are all examples of socially learned vocal displays. The presence of small-world structure in these displays suggests that it is a common feature across multiple species. Network analysis is well-established in the study of language (Ferrer i Cancho, 2010), but has only been applied to a few animal species:

several oscine species with complex songs, and now humpback whales (Chapters 4). Quantifying network structure in other culturally learned vocalizations such as killer whale dialects (Deecke *et al.*, 2000) would help determine how common small-world structures are. Further, conducting analyses on simple vocal displays would help determine if small-world structure is a feature of complex vocal learning or if they occur in a wide variety of communication systems and vocal displays. It should be clarified that while humpback whale and bird songs share syntactic features with language in terms of structural arrangement (i.e. the rules that govern how elements can be arranged in a display; Chapter 4; Marler, 1977; Berwick *et al.*, 2011; Kershenbaum *et al.*, 2014), they are not thought to contain syntactic complexity in the linguistic or semantic context seen in human language (Hauser *et al.*, 2002; Fitch *et al.*, 2005; Berwick *et al.*, 2011). In other words, it is believed that only in language does word arrangement impact the message those words convey. However, recent work had provided potential evidence that such "compositional syntax" may be present in non-human species such as Japanese great tits (Suzuki *et al.*, 2016), southern pied babblers (Engesser *et al.*, 2016), and meerkats (Collier *et al.*, 2017). This new evidence, in combination with the results found in this thesis, suggest that there is still much to learn about the role of syntax in both human and non-human communication.

Language, birdsong, and humpback whale song all contain syllables that serve as 'hubs' or connection points within their network structure (Capitán *et al.*, 2012). In human language, these words are often 'function' words such as 'and', 'the', 'is' or 'in' (in English). The equivalent in humpback whale song (Chapter 4) and birdsong (Sasahara *et al.*, 2012; Taylor and Cody, 2015) is the 'hourglass' transition motif, which facilitate diversity in sequences because they can be preceded or followed by a wide variety of other unit types (Sasahara *et al.*, 2012). These central unit types serve as hubs which open the display up to variation in its sequences, similar to the 'hub' words used in human language to make diverse sentence arrangements (Capitán *et al.*, 2012). However, human language has context-free grammar, which means that changing the arrangement of a sentence changes it semantically (i.e. changing the word arrangement changes the meaning of the sentence) (Fitch *et al.*, 2005; Berwick *et al.*, 2011). Displays like the songs of birds and humpback whales have much simpler 'regular' grammar (Kershenbaum *et al.*, 2014). As a result, changes in sequence arrangement most likely retain the same simple, fixed information (Berwick *et al.*, 2011). One-way transitions (preceded or followed by a select few unit types) are the other common type of transition pattern in both birdsong and humpback whale song (Chapter 4). These transitions limit variation by directing the display towards a particular pattern or sequence. Both humpback and songbird displays contain certain features such as deterministic transition motifs and

redundancy in unit usage which suggest stability, while other features such as hourglass transition motifs suggest variability. This leads to a song structure that is both easy to learn through its stability, yet allows for flexibility and for the incorporation of novelty. Balance between these two characteristics is typically important for culturally learned displays such as the songs of both birds (Payne, 1985; Margoliash *et al.*, 1991) and humpback whales (Garland *et al.*, 2011). Displays with stable structure will be easier to learn and thus will spread more quickly between individuals (Lachlan *et al.*, 2004; Claidière and Whiten, 2012; de Waal, 2013). However, the appeal of novelty is often a driving force behind cultural changes and therefore displays must be flexible enough to accommodate that (Cerchio *et al.*, 2001; Noad, 2002).

Small-world network structure is a key feature of in birdsong, humpback whale song, and language which could provide insight into their development. All of these species demonstrate statistical learning which allows them to identify and learn patterns in their respective displays (Romberg and Saffran, 2010; Feher *et al.*, 2016; Garland *et al.*, 2017a). Development of both human speech and birdsong share commonalities such as similar neural mechanisms, an early latent learning period, and imitation through exposure (Doupe and Kuhl, 1999; Bolhuis *et al.*, 2010; Berwick *et al.*, 2011). In contrast, humpback whales must continuously learn new songs as the pattern changes from year to year. As a proposed breeding display (Payne and McVay, 1971; Winn and Winn, 1978; Payne *et al.*, 1983; Helweg *et al.*, 1992), song development and onset is likely to occur around sexual maturity (5-10 years old) (Clapham, 1996; Garland, 2011). Developmental patterns in vocal learning often provide an understanding of their evolutionary processes. Commonalities allow for comparison of complex vocal learning across taxa.

6.6 Future directions

Both the creation of a representative acoustic dictionary and the quantification of unit acoustic similarity are novel and addressed gaps in signal classification (Chapter 2, Allen *et al.*, 2017). Current quantitative techniques such as self-organizing maps or random forest analyses require a full suite of acoustic measurements from every sound. An acoustic dictionary allowed for the advantage of a quantitative element allowing robust and repeatable classification of units prior to transcription (Chapter 2, Allen *et al.*, 2017). Transcriptions would otherwise require the measurement of acoustic features for every unit in every song cycle in order to incorporate this quantitative classification. Acoustic features of units were quantified through the Cartesian distances between units in the dictionary, providing a novel means to weight the Levenshtein distance analyses based on acoustic similarity (weighted analysis detailed in Garland *et al.*, 2017).

Other options for refining the weighting of an LSI analysis include Eucledian distances between units based on acoustic features (similar to the Cartesian distance cost matrix) or a customized cost matrix (Allen *et al.*, 2017; Garland *et al.*, 2017b). There is potential for application of these novel methods to other humpback whales populations or the vocal displays of other species. A dictionary would need a representative subsample from the study display with recordings of high enough quality to accurately measure pertinent acoustic features. While this method does not eliminate subjectivity, it does provide a robust and repeatable means of classifying and transcribing vocal sequences for fine-scale study.

A limitation of the weighted LSI was that sequence length could skew the results. Two sequences of similar lengths often had a higher LSI value (and thus a higher degree of similarity) compared to sequences containing similar unit types but different lengths (Garland *et al.*, 2017b). The complexity results of Chapter 3 partially explained this. Themes became more complex as they evolved through the insertion of either new unit types or increased repetitions of present ones. On the other hand, two unrelated themes of similar lengths often resulted in more substitutions than insertions or deletions. Insertions are a more drastic change in the weighted LSI analysis than substitutions, and therefore are given a higher penalty (Garland *et al.*, 2017b). Due to this limitation, weighted LSI analysis at a unit sequence level must be applied carefully. It reliably verifies distinct themes (demonstrated in Chapter 3 and by Murray et al, 2016) or identifies the same theme in different populations (demonstrated in Chapter 5). However, caution should be exercised in tracking the evolution of a theme due to the disproportionate number of insertions in evolving themes. For this reason, evolving themes were defined using a threshold of at least 20% similarity in addition to being qualitatively identified as related (Chapter 3). Garland *et al.* (2017b) suggests consideration of the location and arrangement of the theme within the song as a way to counter this limitation. I additionally suggest that future work should attempt to account for the retention of units within an evolving theme. For example, if a theme has sequence ABC and evolves to AABCD, the new theme has retained three units from the original theme in the same order. A 'bonus' for retained units or sequences could counter the penalty of insertions and better reflect similarity between evolving theme. Another strategy would be to markedly reduce the weighting of insertions (or deletions) if the preceding unit was the same, so effectively increasing or reducing the repetition of a unit type rather than a more substantive change involving a different unit type.

The fine-scale song features identified in this thesis should be quantified in additional song types across the remaining South Pacific populations. This will determine if these patterns in fine-scale song transmission remain consistent across several populations. Relative complexity measures and network structures from the same song type in multiple populations would provide strong evidence for inter-population song learning mechanisms. If song transmission between east Australia and New Caledonia is indicative of subsequent transmission further eastward, then complexity levels of themes should remain comparable throughout large-scale cultural transmission (Chapter 5). This unique cultural phenomenon in the South Pacific provides the opportunity to assess features of a song when it is sung by as many as seven populations (Garland *et al.*, 2011; Garland *et al.*, 2015).

If the analyses performed here can be expanded to include more consecutive years from New Caledonia, it can be determined if complexity has the same relationship that occurs in east Australia (i.e. increases during evolutions and decreases during revolutions). Based on the patterns seen in east Australia (Chapter 3), it is hypothesized that New Caledonia will demonstrate a similar relationship. Furthermore, a larger sample size would establish a more conclusive pattern regarding the way complexity changes in analogous song types between east Australia and New Caledonia. Chapter 5 analysed two song types (Teal and Orange) in two consecutive years, both of which were cultural revolution events. Complexity of the song as a whole could only be compared descriptively due to small sample size. Increasing the sample size to include more years (with both evolutions and revolutions) will better determine if the patterns found between populations are indicative of true relative complexity and if those patterns hold true when a song is either particularly simple or particularly complex.

The ability to learn shared songs with increasing complexity may have limitations, explaining why cultural revolution events replace the existing song type with a simpler one. A way to explore this would be to quantify complexity in the west Australian versions of the songs, which appear to be the source of the revolutionary song types identified to date (Noad *et al.*, 2000; Rekdahl, 2012). If the song complexities are equivalent, the east Australian population may pick up the west Australian song because their own has reached the limits of their learning ability and the new song is simpler. Alternatively, if complexity is lower in the east Australia version, they may simplify the song during revolution events due to constraints on their ability to learn such a large amount to novel material. This could be due to cognitive limits on learning or may be due to more proximate factors such as relatively limited acoustic contact between populations and thus

only brief windows for learning. New Caledonia's version of the songs maintained complexity at the theme-level during transmission from east Australia, suggesting acoustic contact which facilitates high fidelity learning of complex arrangements (Chapter 5). Song-level complexity was shown to decrease somewhat, though this was attributed to the differences in phrase repetitions. As phrase repetitions can vary, potentially based on social and behavioural context (Smith, 2009), and may be due to differences between the context of breeding ground singing (New Caledonia) and migratory singing (Peregian). This would provide another interesting area of future research.

Cultural revolution events have not been documented thus far in the populations of any other ocean basins. Instead, other populations appear to have songs that are continually evolving (Payne *et al.*, 1983; Payne and Payne, 1985; Darling *et al.*, 2014). Future research should quantify fine-scale features of populations outside the South Pacific to determine which features remain part of the songs regardless of the population they belong to and how these features change without the cultural revolutions seen in the South Pacific. It is already well established that all humpback whale song contains the same hierarchical structure and that songs progressively evolve over time (Payne and McVay, 1971; Payne *et al.*, 1983; Payne and Payne, 1985; Cholewiak *et al.*, 2013; Darling *et al.*, 2014). However, structural features beyond this hierarchy have not yet been quantified at a fine-scale level. The qualitative nature of most research on structural features has lacked standardization, hindering effective comparison of song features across populations with limited or absent acoustic contact. The novel complexity measure developed here (Chapter 3) and the application of network analyses (Chapter 4) would allow for quantitative comparison of song features across any humpback whale population (as demonstrated in Chapter 5), regardless of their ocean basin.

6.7 References

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Appendices

Appendix 1: Quantitative verification of themes

Each figure in this section (Fig.s A1.1-15) displays an average-linkage hierarchical dendrogram from the Levenshtien Similarity Index (LSI) scores from each theme per year. Each letter represents a theme, with letters indicating the population the song came from (EA or NC) and the two digit number preceding the letter indicating the year in which the theme occurred (02-15). All repetitions of each theme were grouped by the cluster analysis onto separate primary branches of the dendrogram. Themes with a number following the letter indicate where a single theme was separated into two distinct versions that were divided onto separate branches. This was common as themes often had multiple versions, or sub-phrases

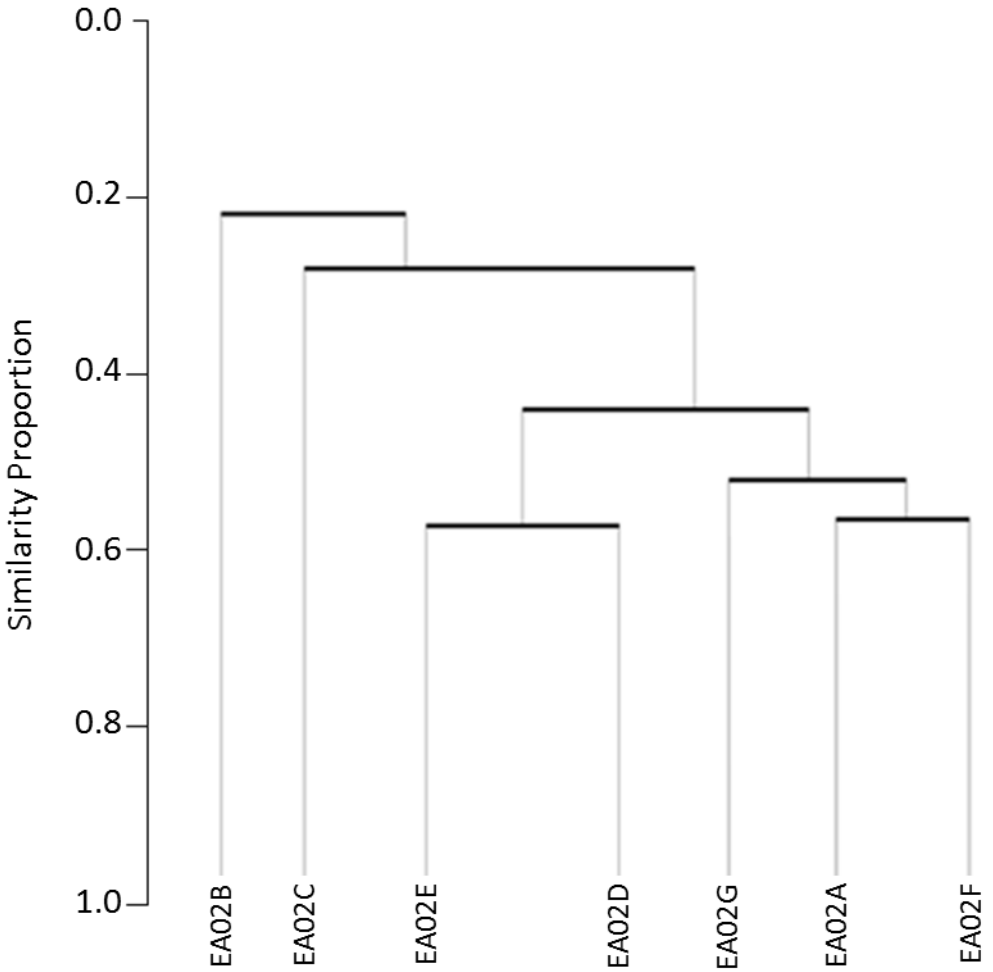


Figure A1.1 East Australia 2002 dendrogram of themes

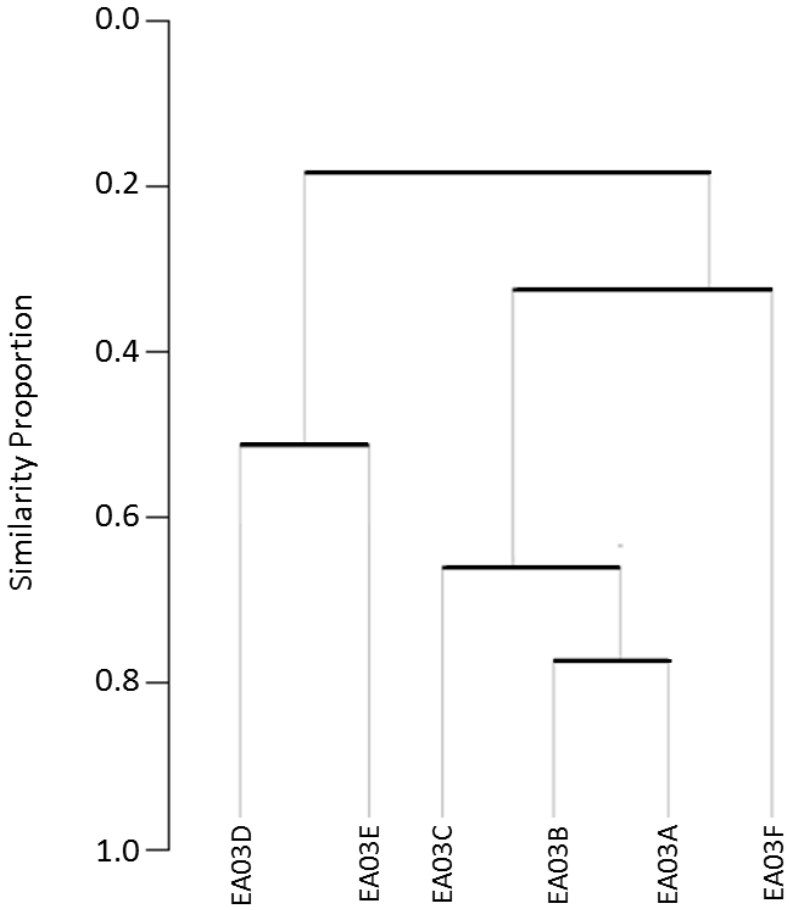
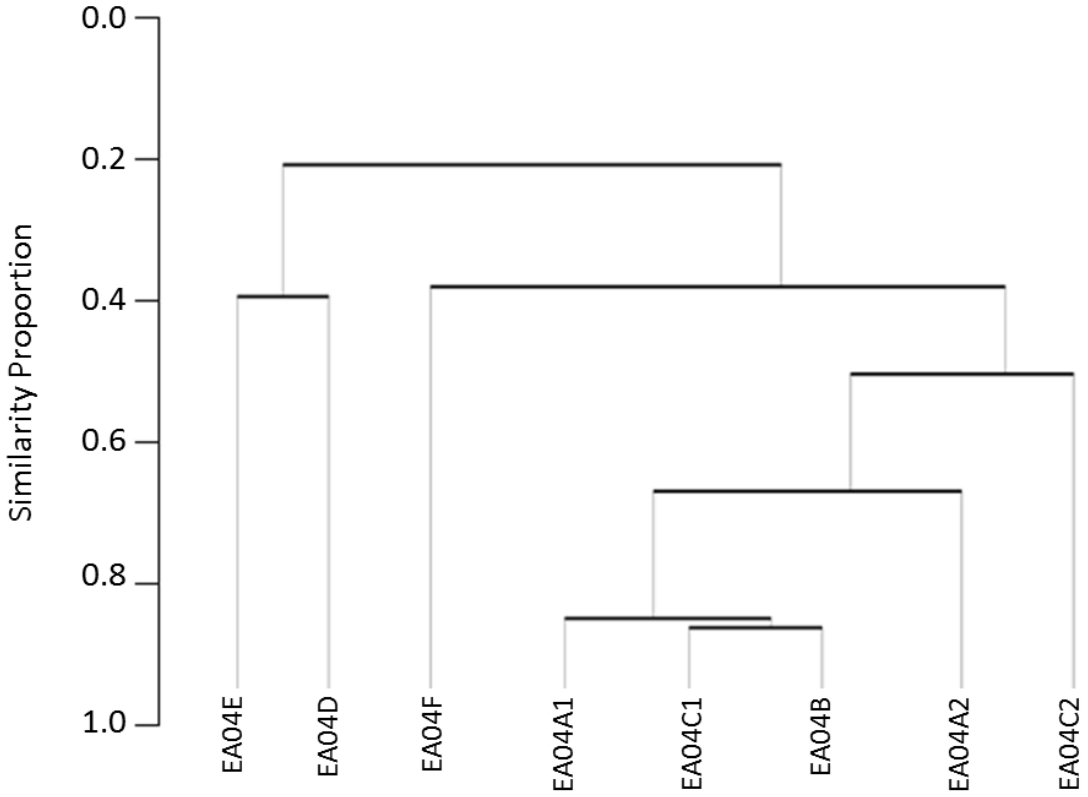


Figure A1.2 East Australia 2003 dendrogram of themes



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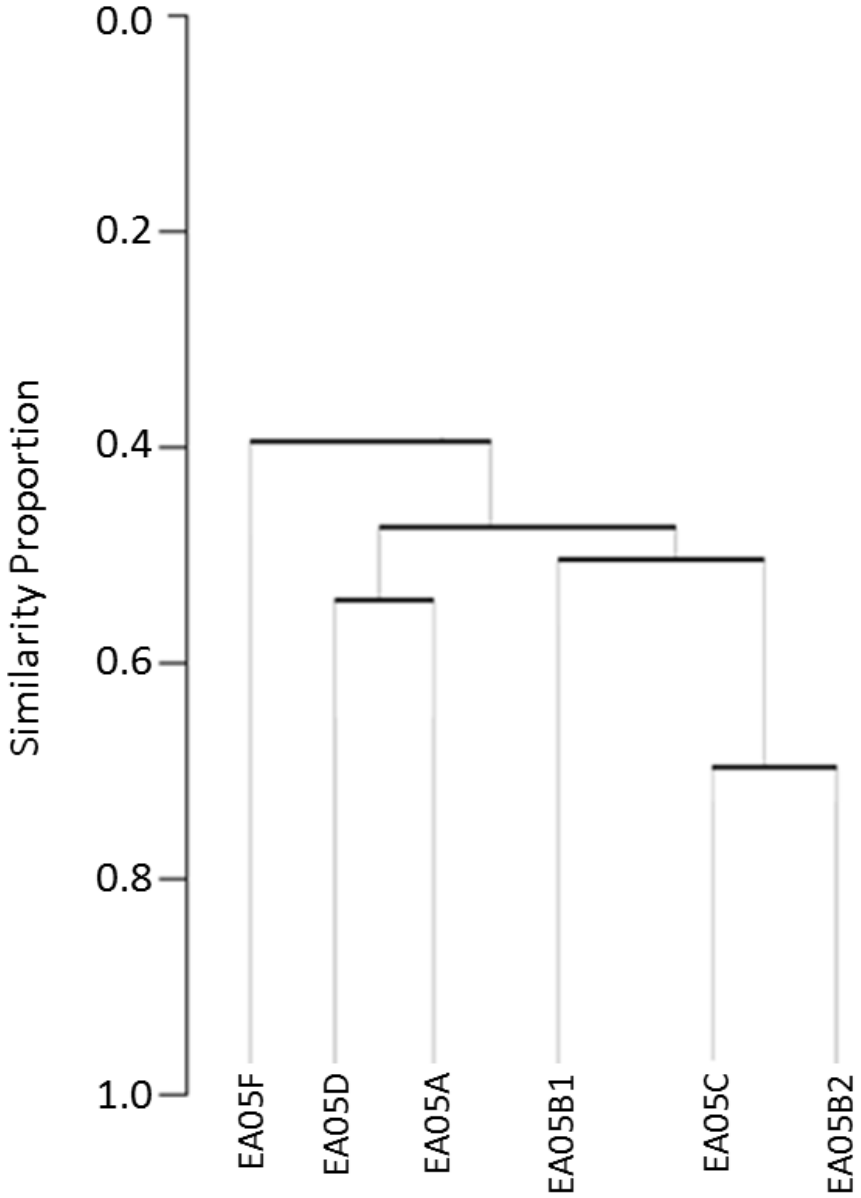

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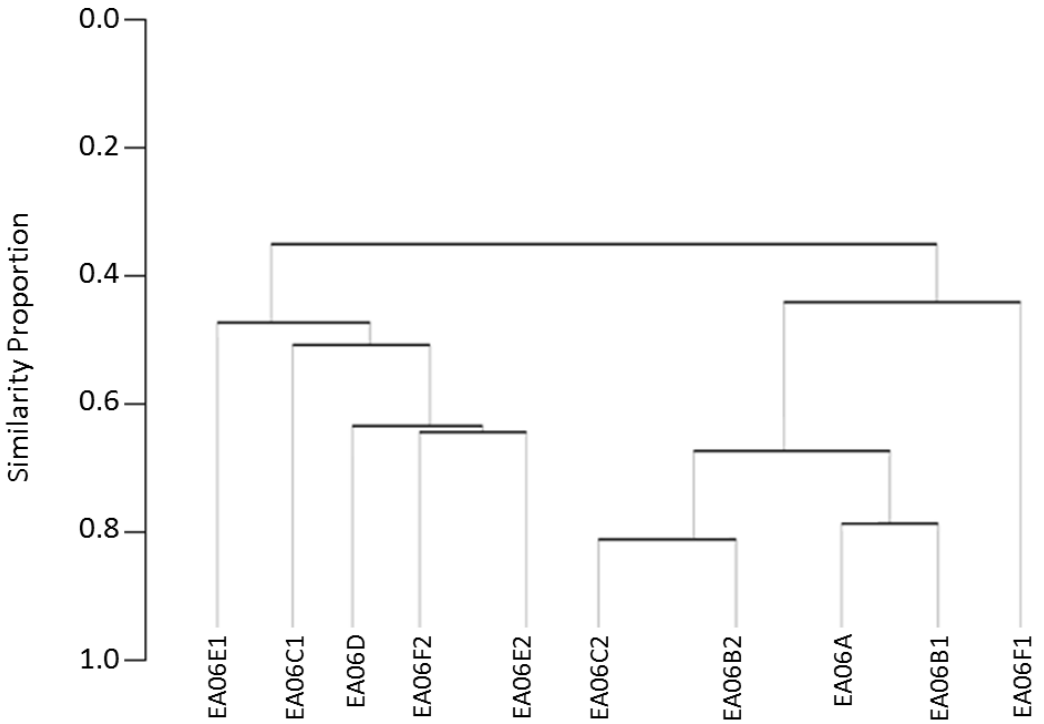


Figure A1.5 East Australia 2006 dendrogram of themes

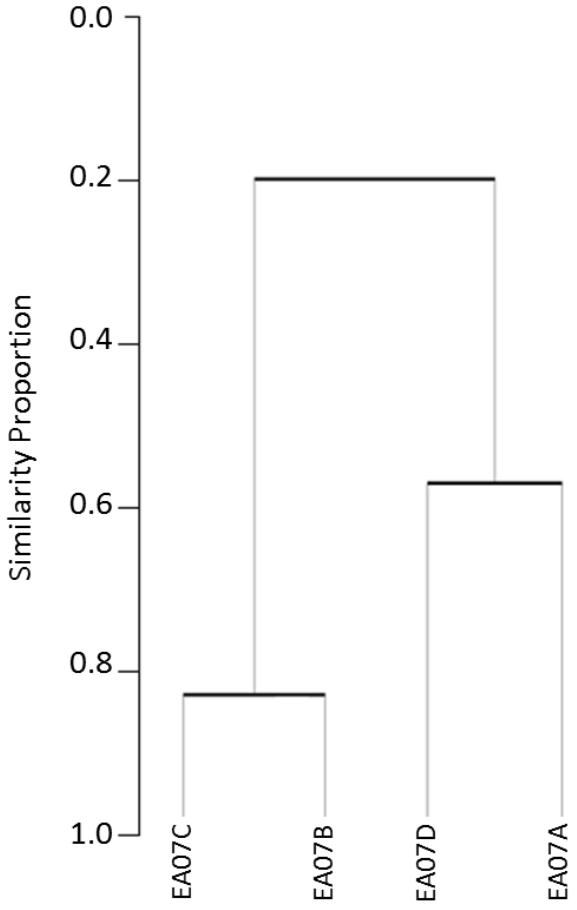


Figure A1.6 East Australia 2007 dendrogram of themes

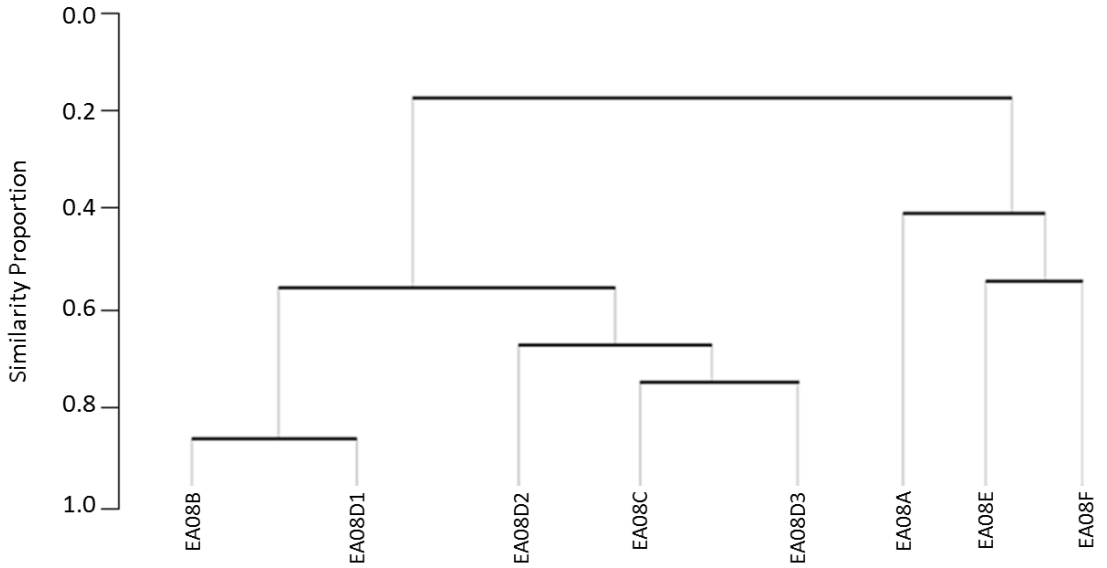


Figure A1.7 East Australia 2008 dendrogram of themes

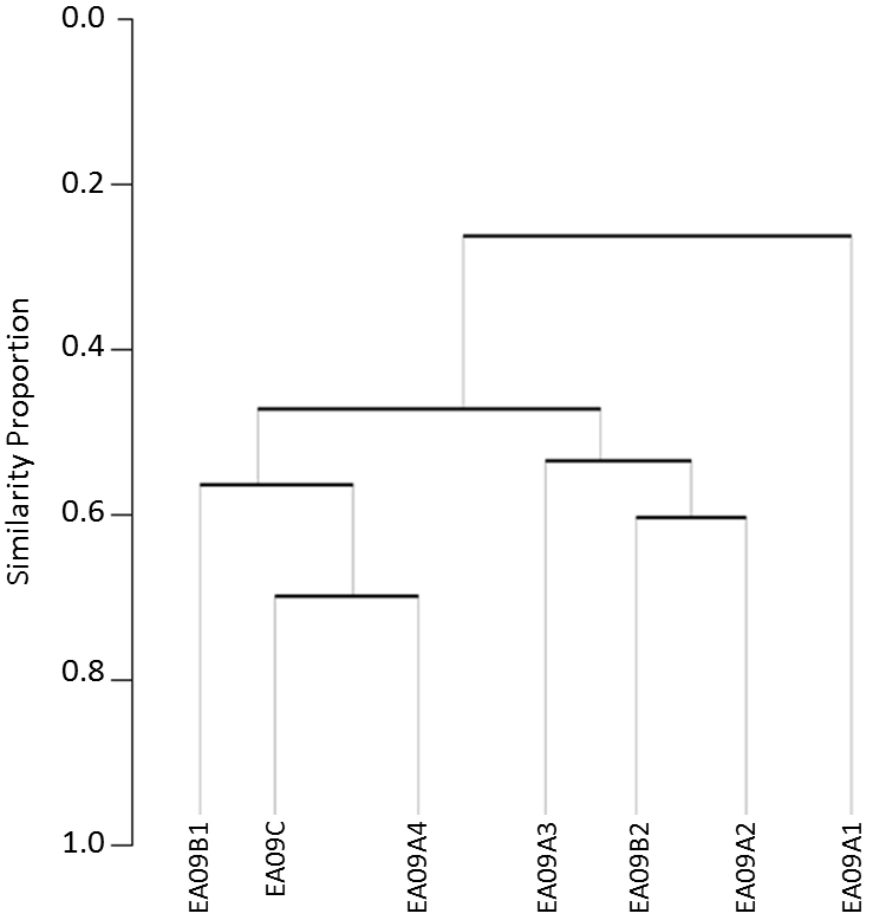


Figure A1.8 East Australia 2009 dendrogram of themes

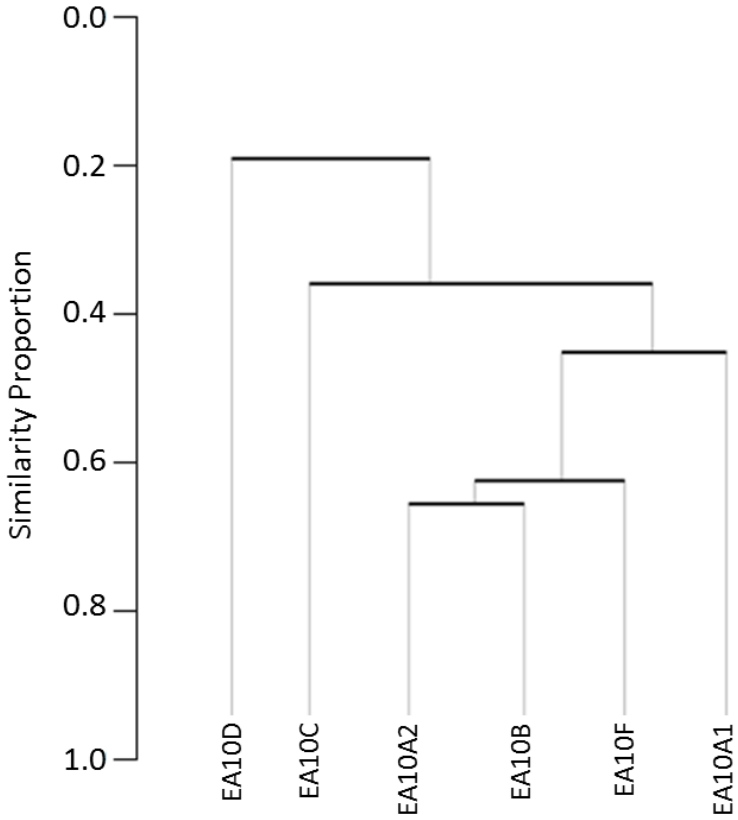


Figure A1.9 East Australia 2010 dendrogram of themes

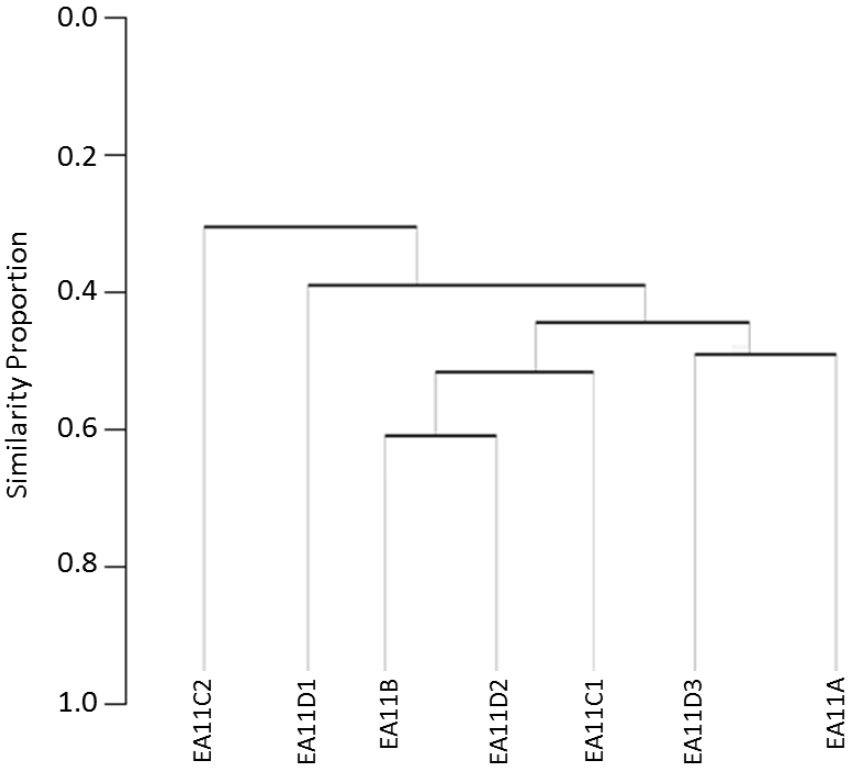


Figure A1.10 East Australia 2011 dendrogram of themes

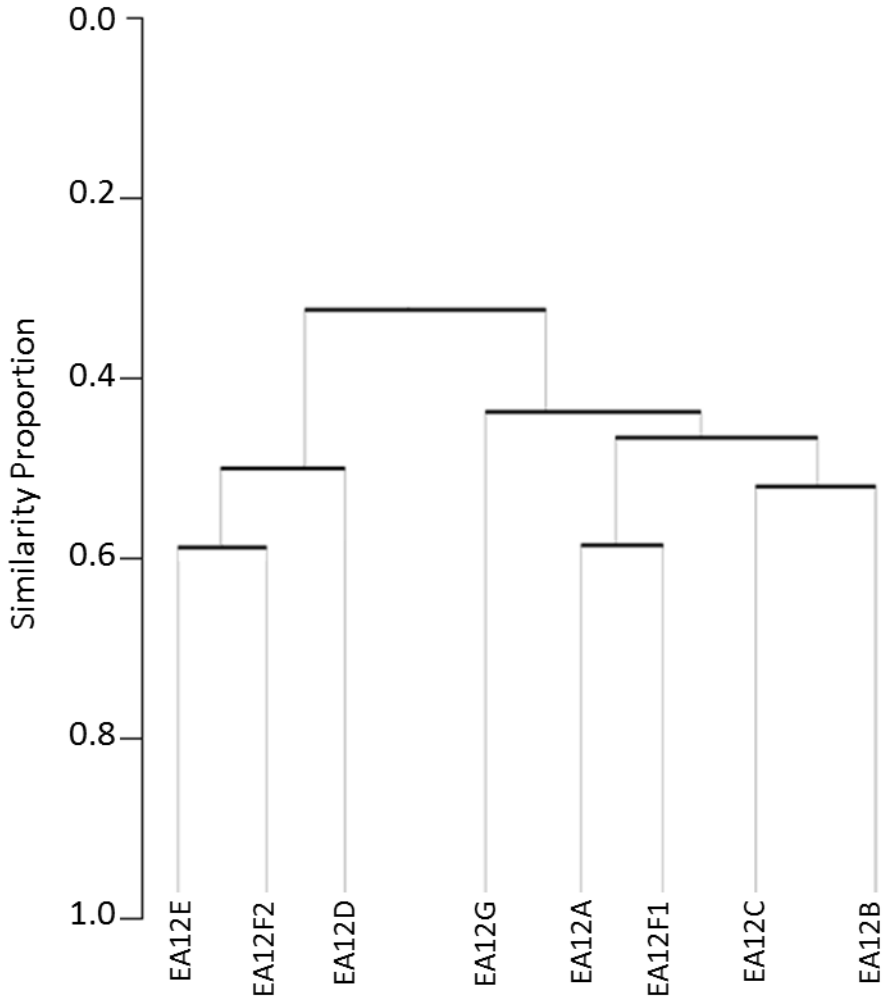


Figure A1.11 East Australia 2012 dendrogram of themes

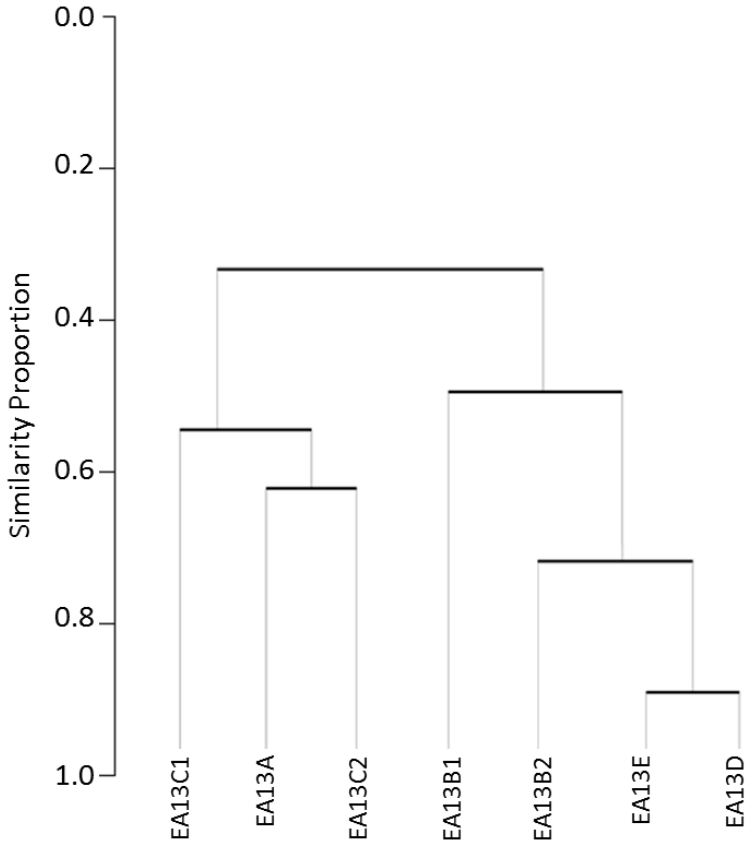


Figure A1.12 East Australia 2013 dendrogram of themes

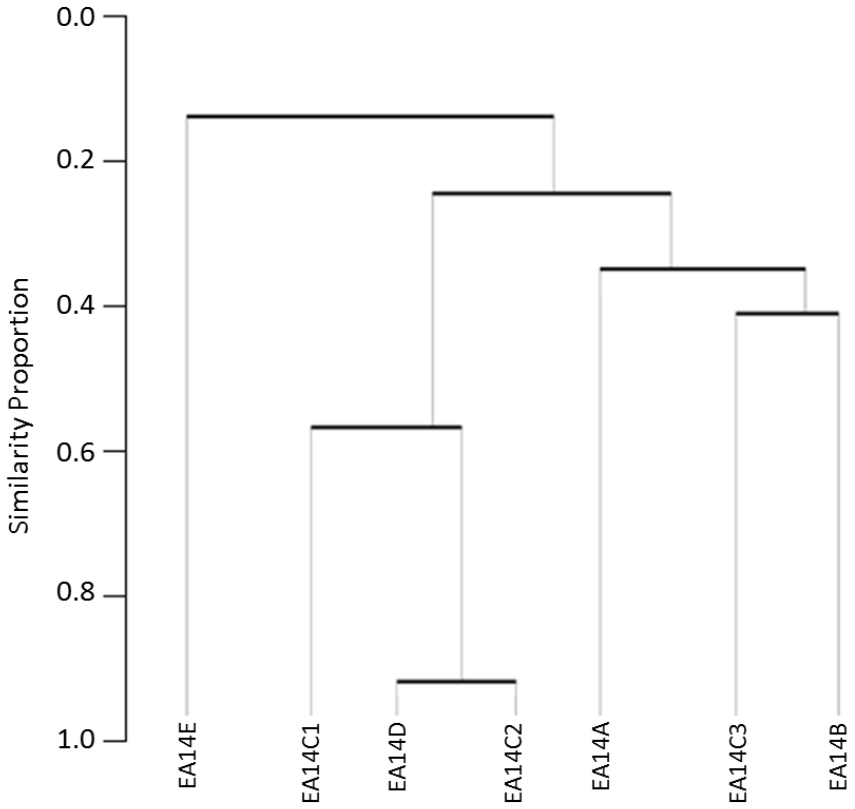


Figure A1.13 East Australia 2014 dendrogram of themes

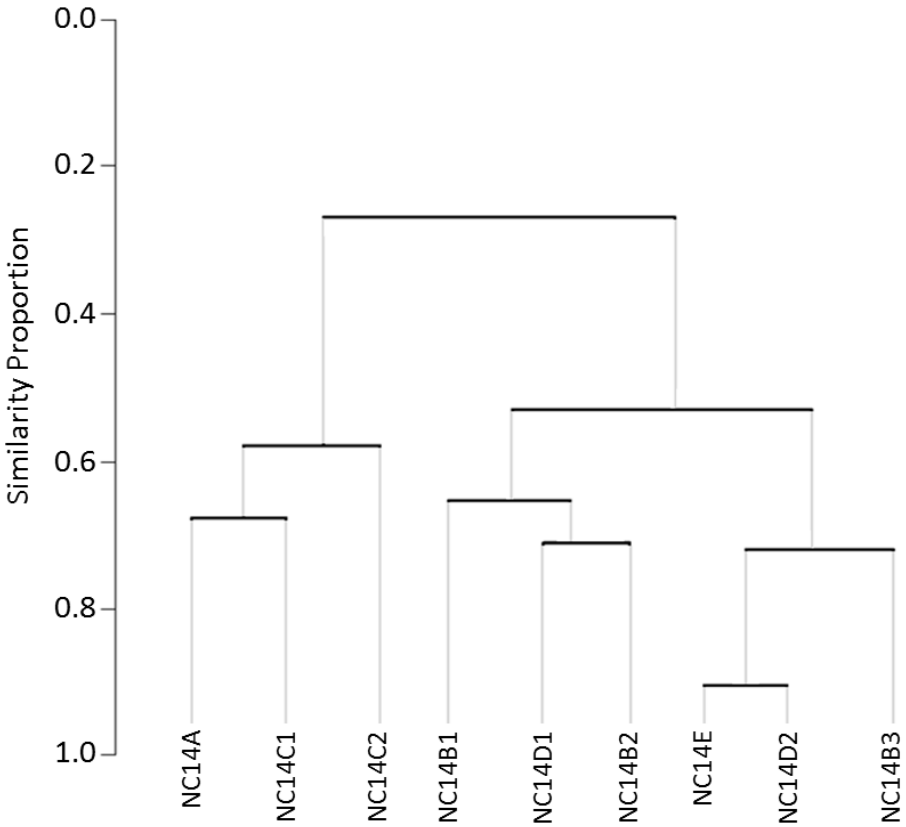


Figure A1.14 New Caledonia 2014 dendrogram of themes

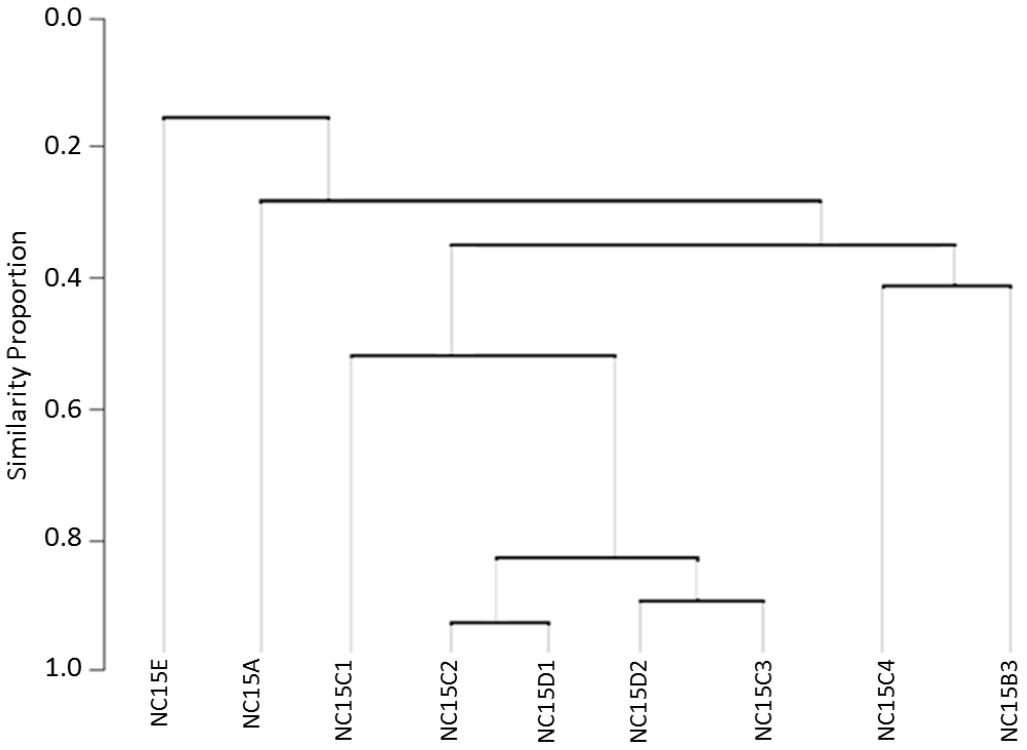


Figure A1.15 New Caledonia 2015 dendrogram of themes

Appendix 2: Evolving themes

Spectrograms are shown for all theme evolutions from 2002-2014 referenced in Figure 3.2 with time (s) on the x-axis and frequency (Hz) on the y-axis. For example, Fig. A2.1 shows the evolution of themes EA03A, EA04A, and EA05A. Theme EA03A evolves into Theme EA04A from 2003 to 2004 through the addition of a unit. This increases duration and both the total number of units and the total number of unique units for that theme increased from two units to three units. From 2004 to 2005, Theme EA04A evolves into Theme EA05A by adding two more short units and repeating a sequence of three units. This increased duration, as well as the total number of units from three to eight and the total number of unique units from three to four.

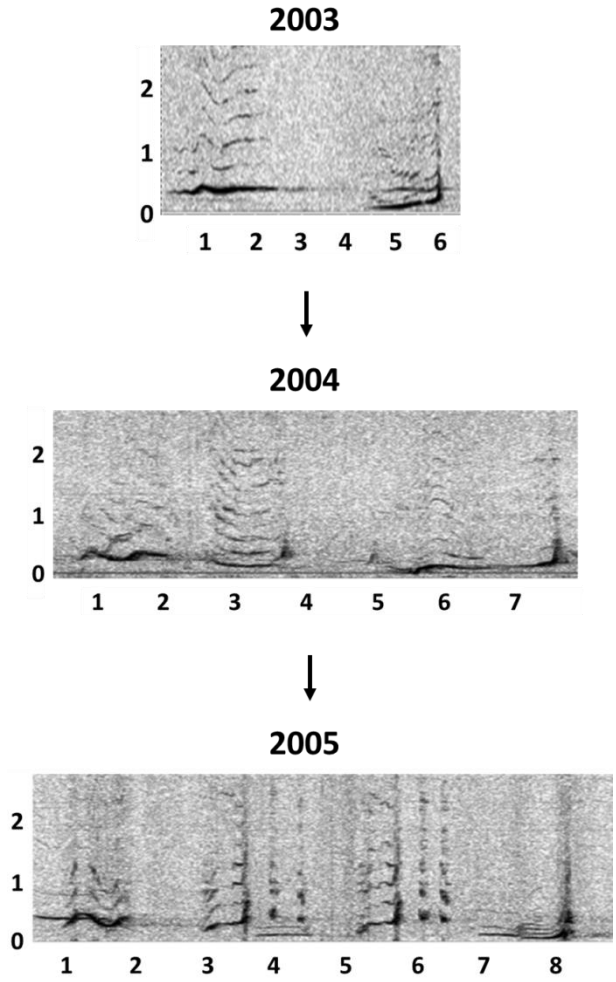


Figure A2.1 Evolving themes EA03A, EA04A, and EA05A from 2003-2005

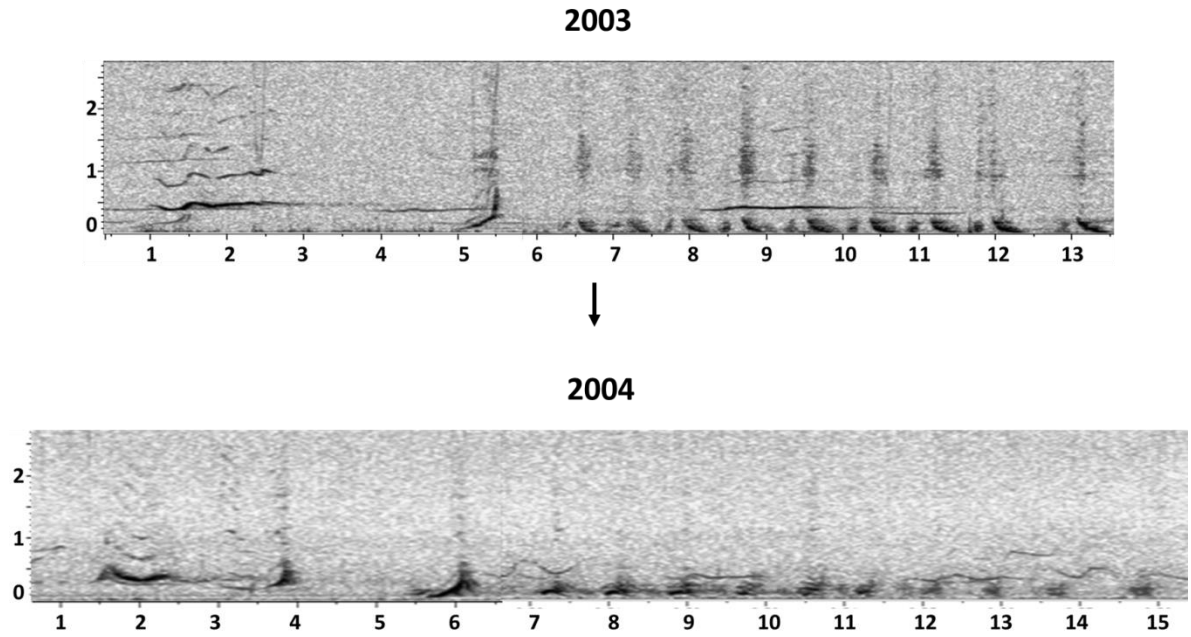


Figure A2.2 Evolving themes EA03D and EA04D from 2003-2004

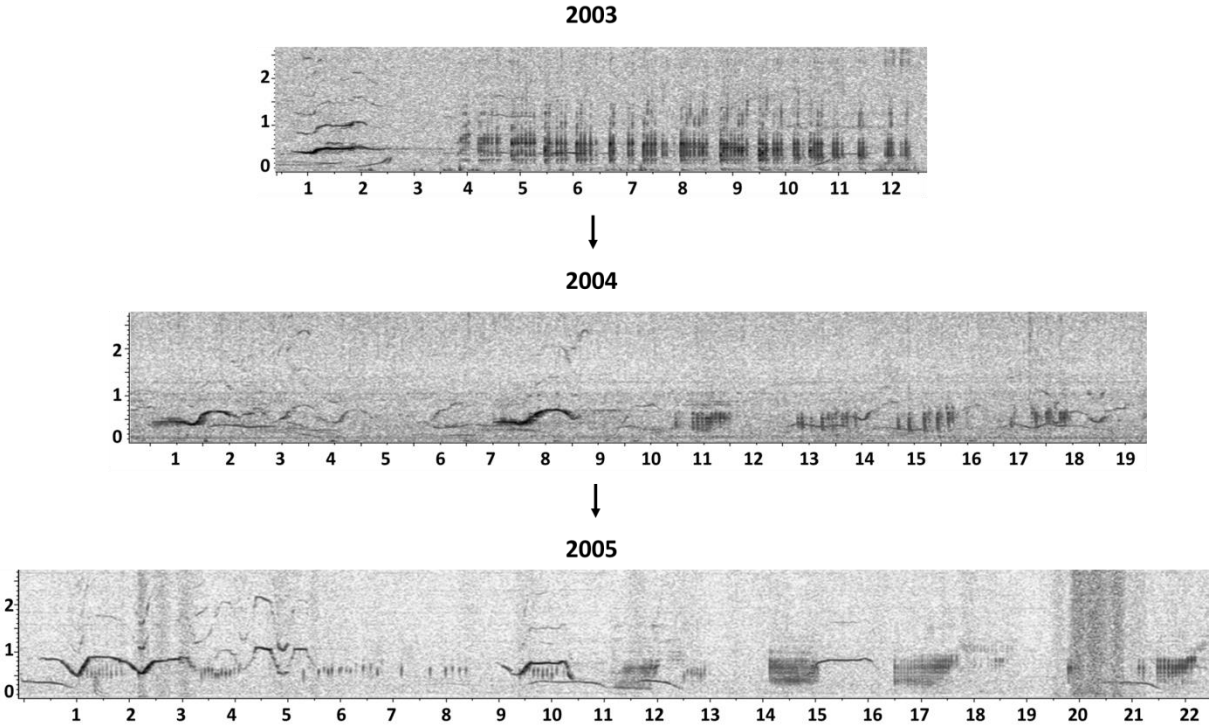


Figure A2.3 Evolving theme EA03E, EA04E, and EA05E from 2003-2005

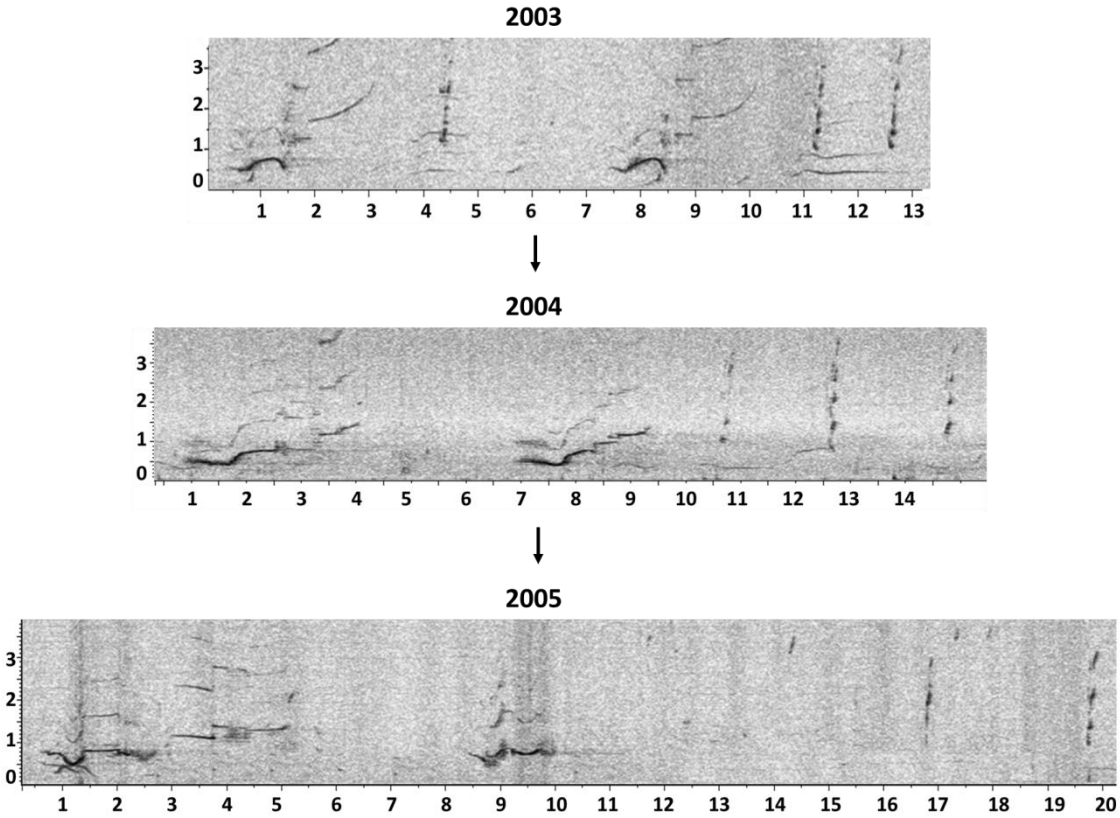


Figure A2.4 Evolving themes EA03F, EA04F, and EA05F from 2003-2005

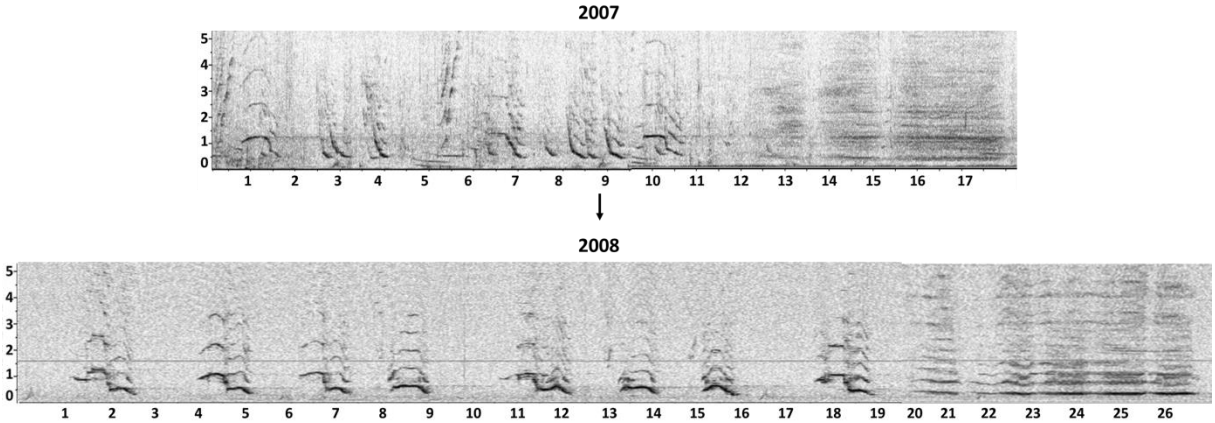


Figure A2.6 Evolving themes EA07A and EA08A from 2007-2008

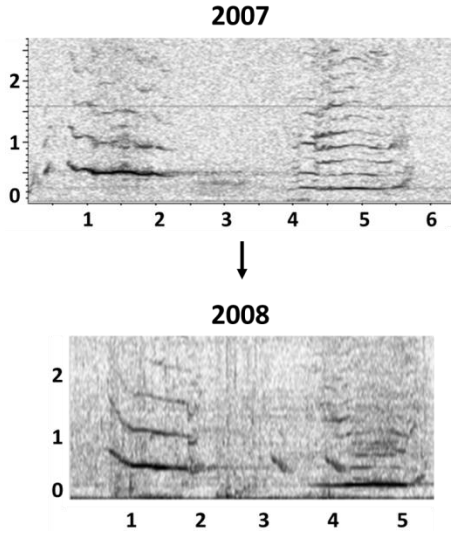


Figure A2.5 Evolving themes EA07B and EA08B from 2007-2008

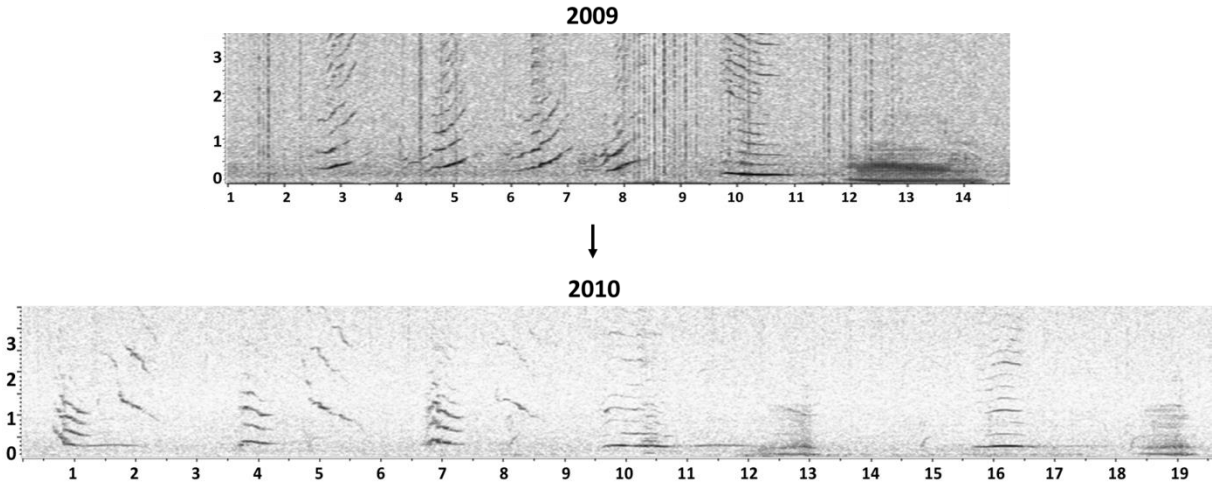


Figure A2.6 Evolving themes EA09A and EA10A from 2009-2010

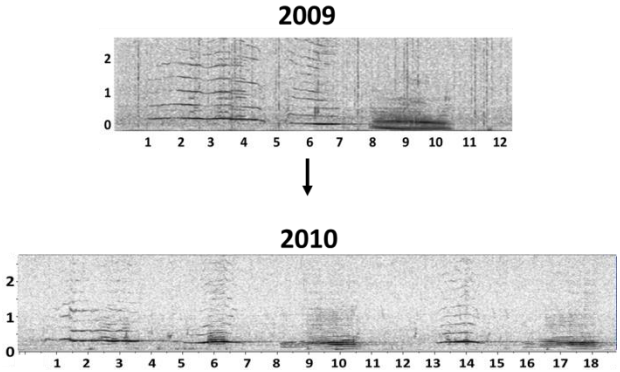


Figure A2.7 Evolving themes EA09B and EA10B from 2009-2010

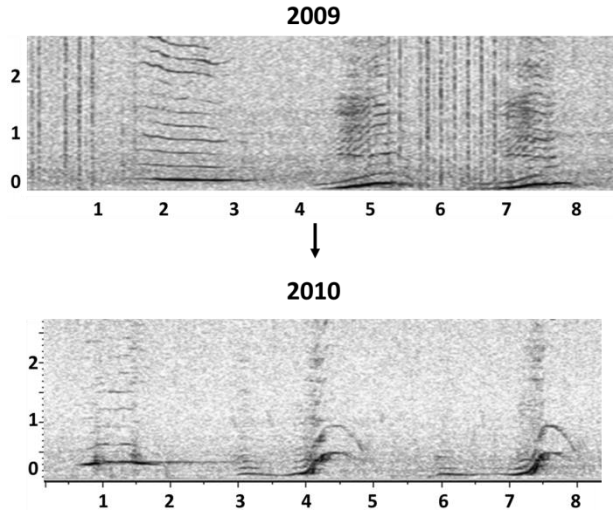


Figure A2.8 Evolving themes EA09C and EA10C from 2009-2010

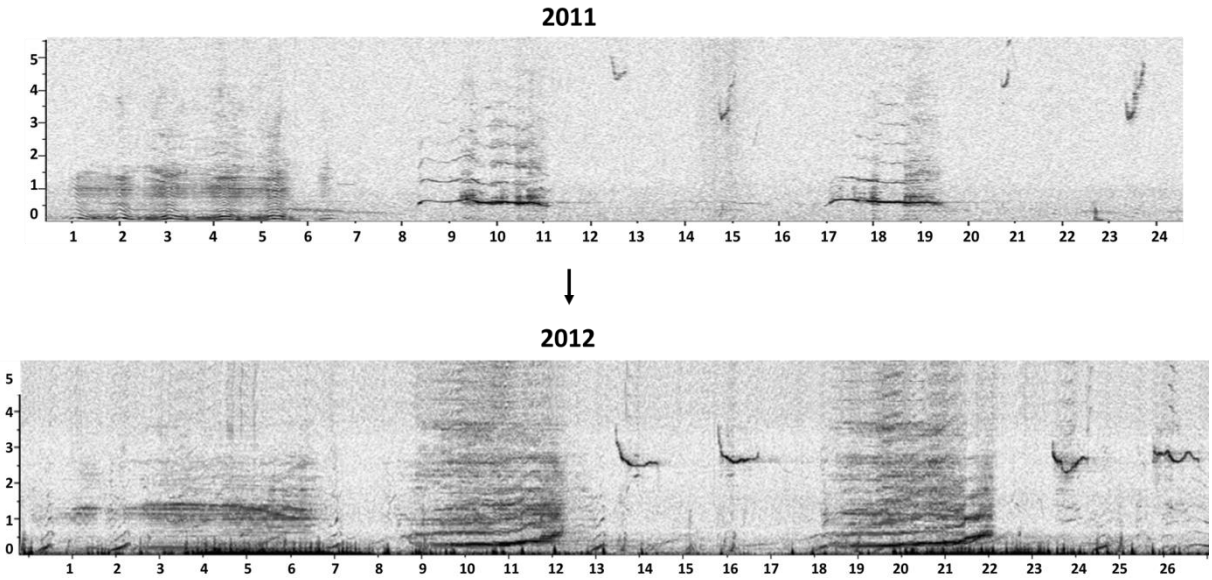


Figure A2.9 Evolving themes EA11A and EA12A from 2011-2012

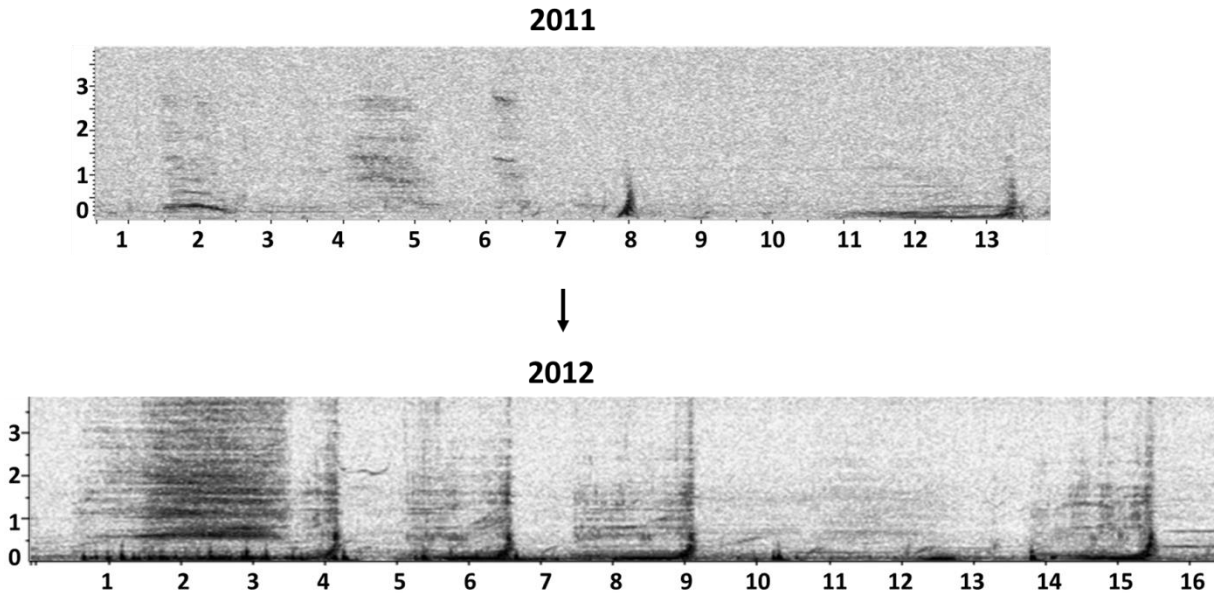


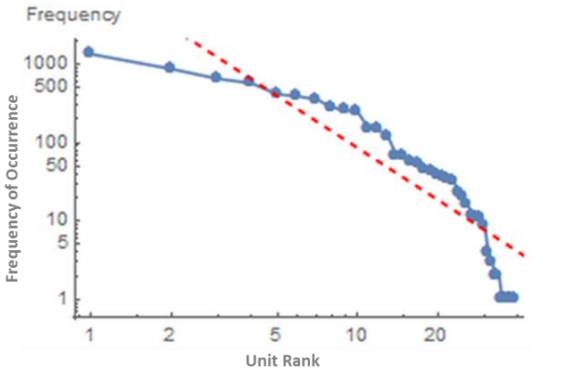
Figure A2.10 Evolving themes EA11C and EA12C from 2011-2012

Appendix 3: Network features

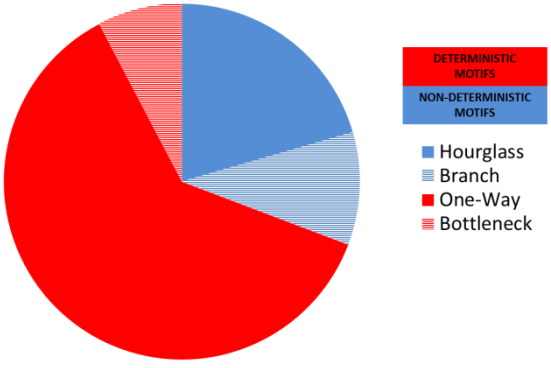
The a) directed network models, b) distribution of unit usage, and c) proportions of transition motifs for each year separately and all years combined. S=small-world coefficient. Each network model has circles (nodes) to reflect unit types, arrows to indicate direction of transition, and line thickness indicates the frequency of the transitions. Small-world themes are circled in different colours. Unit usage is a logarithmic distribution of rank of unit use and frequency of occurrence with a dashed regression line of best fit. Transition motifs are separated into each of the four motif types (one-way, hourglass, branching, bottleneck). Deterministic transitions are in red, non-deterministic transitions are in blue

2002 Network features

a)



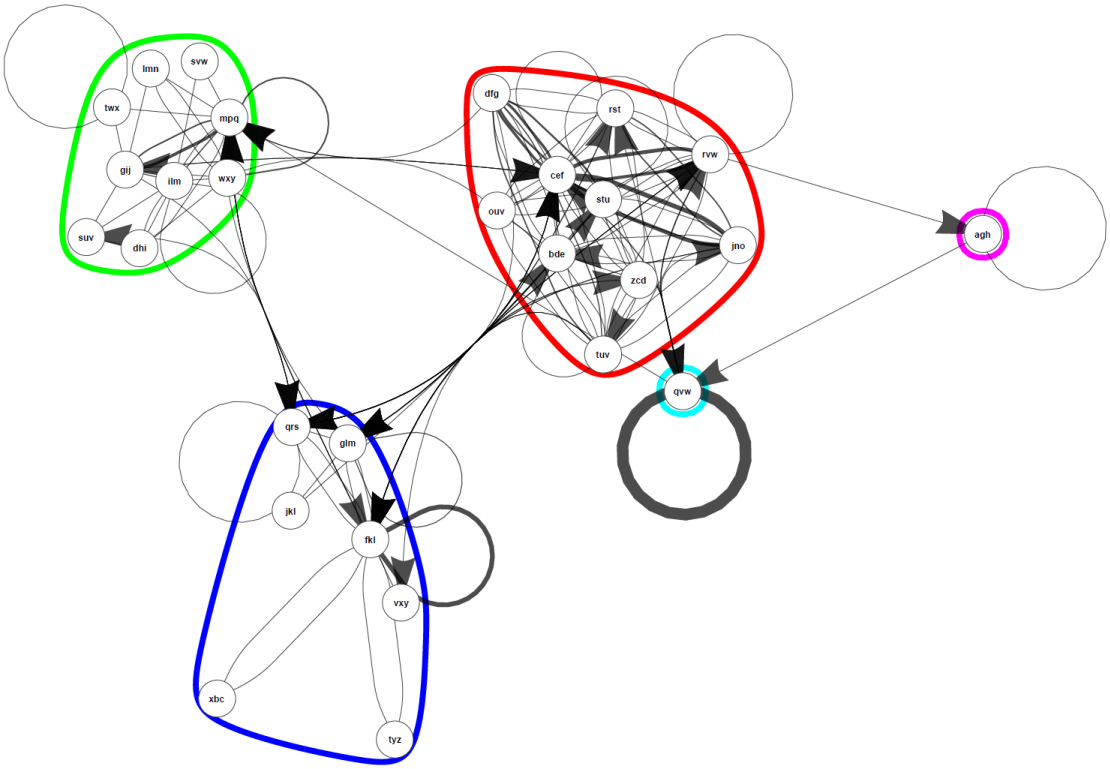
b)



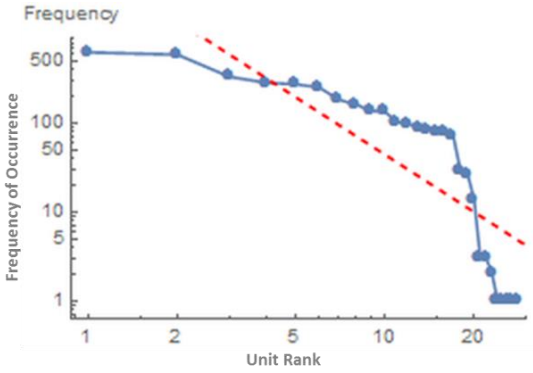
c)

Figure A3.1 Network features for 2002 (S=3.3, N=36)

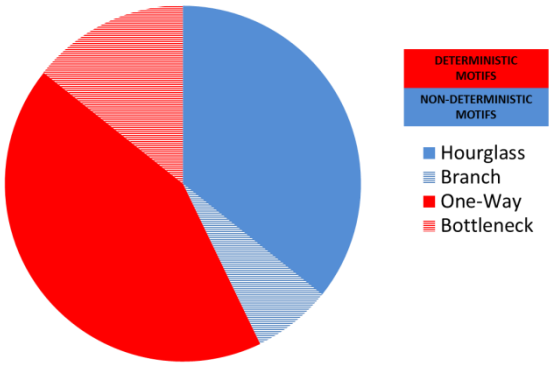
2003 Network features



a)



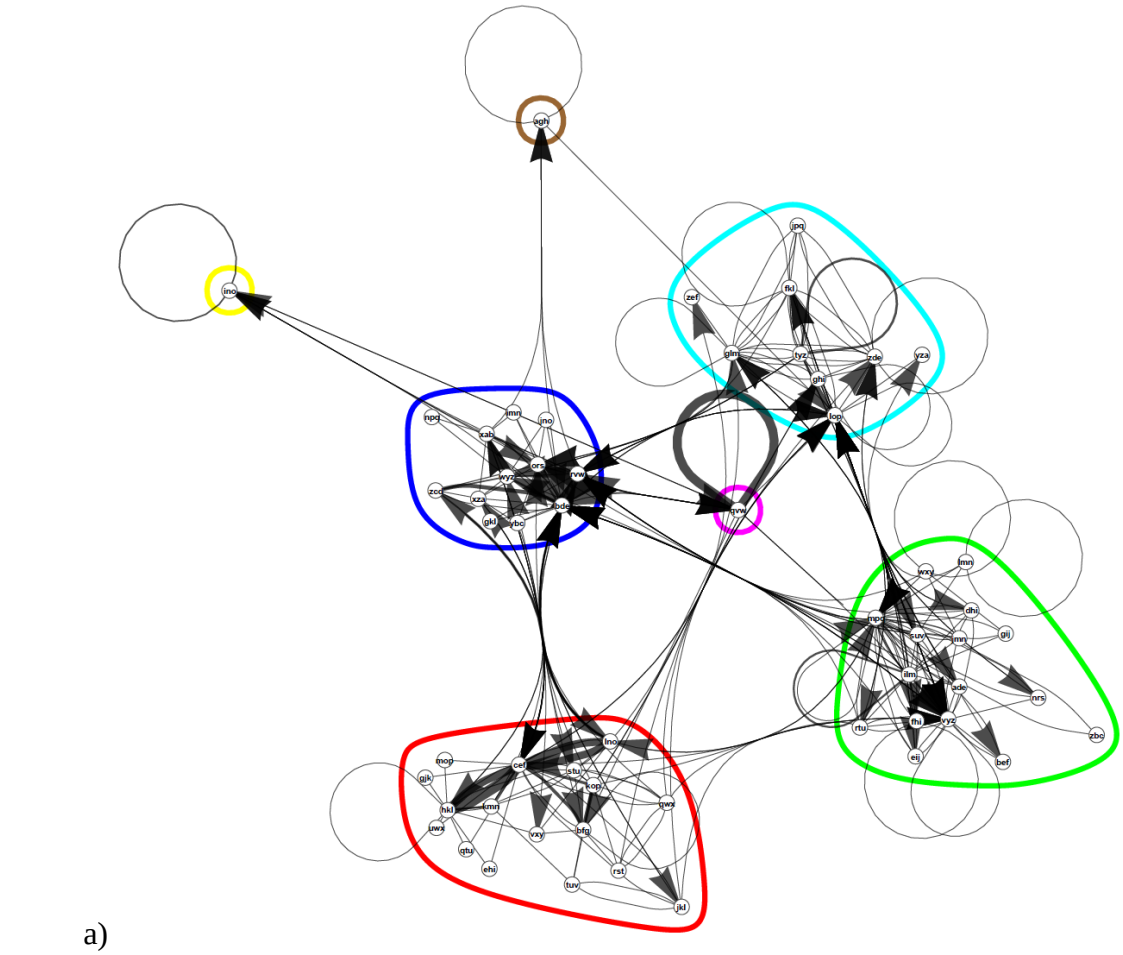
b)



c)

Figure A3.2 Network features for 2003 (S=1.7, N=36)

2004 Network features



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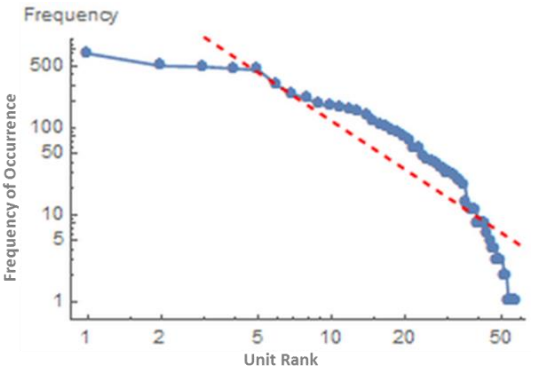

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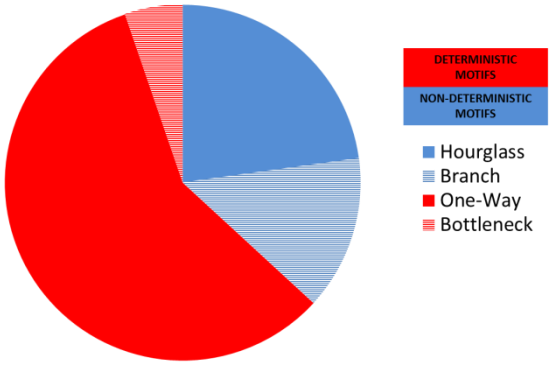
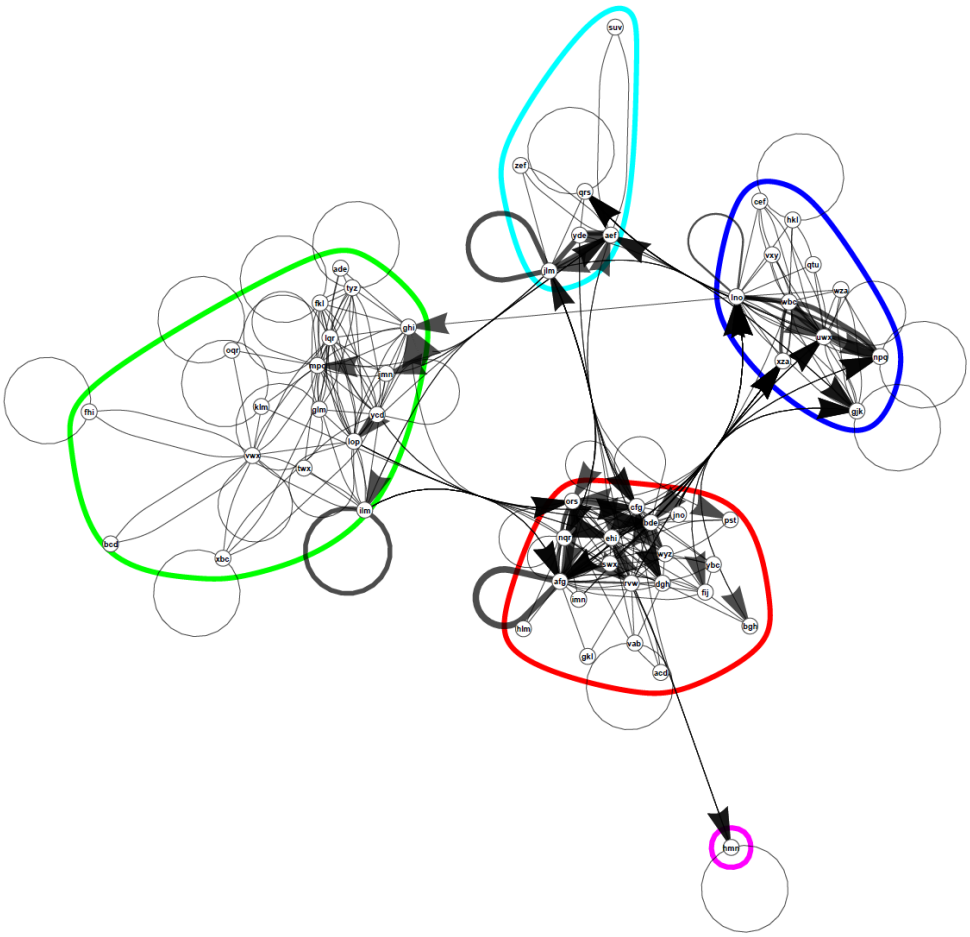


c)

Figure A3.3 Network features for 2004 (S=4.2, N=36)

2005 Network features



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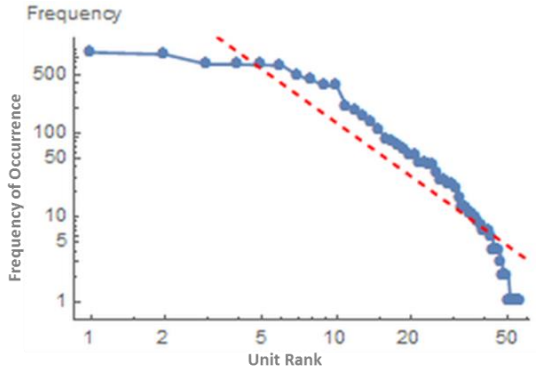

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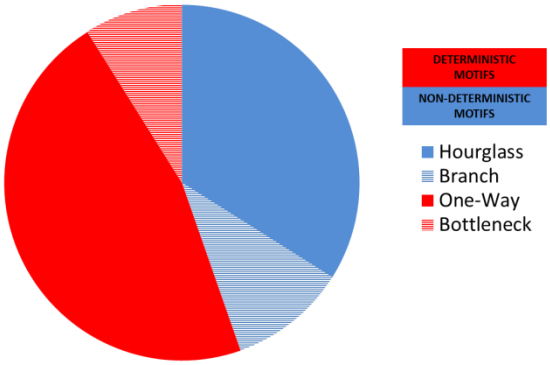
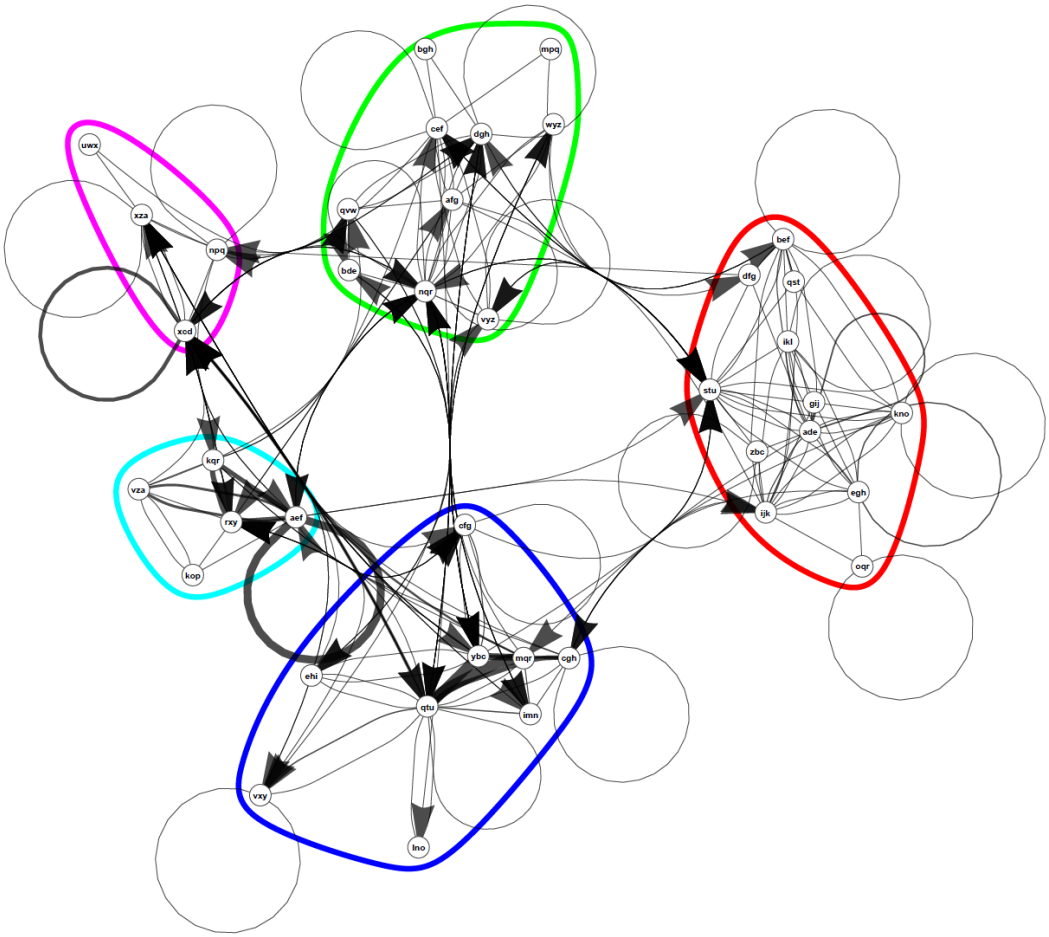


c)

Figure A3.4 Network features for 2005 (S=3.8, N=36)

2006 Network features



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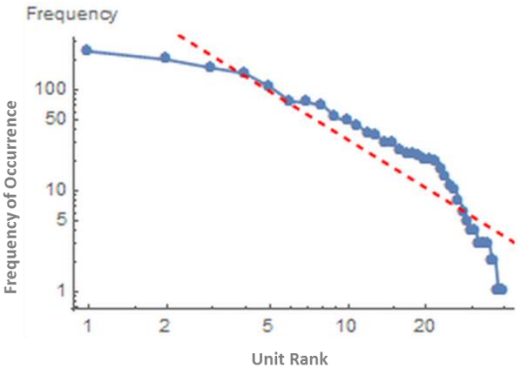
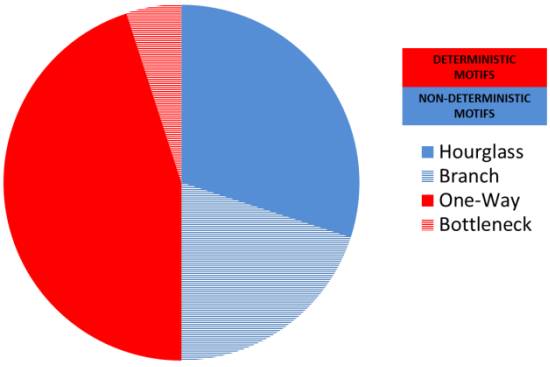


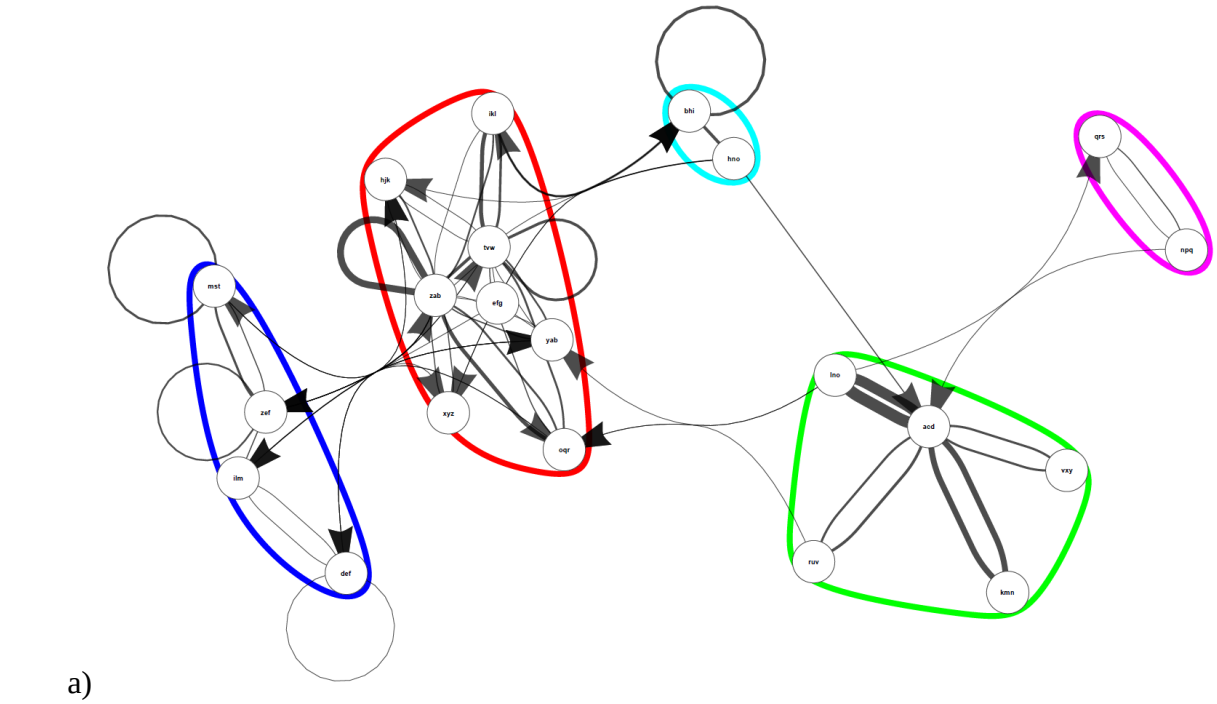
b)



c)

Figure A3.5 Network features for 2006 (S=2.2, N=12)

2007 Network features



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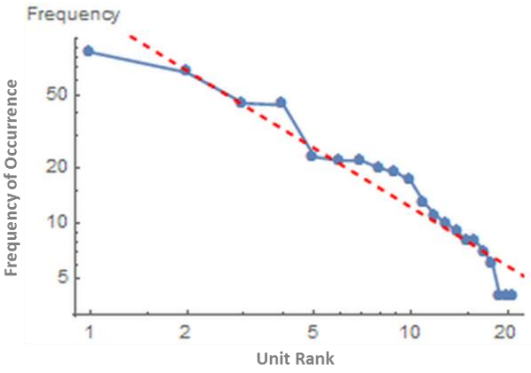
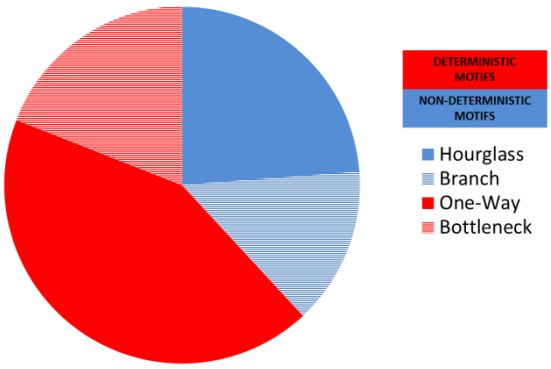


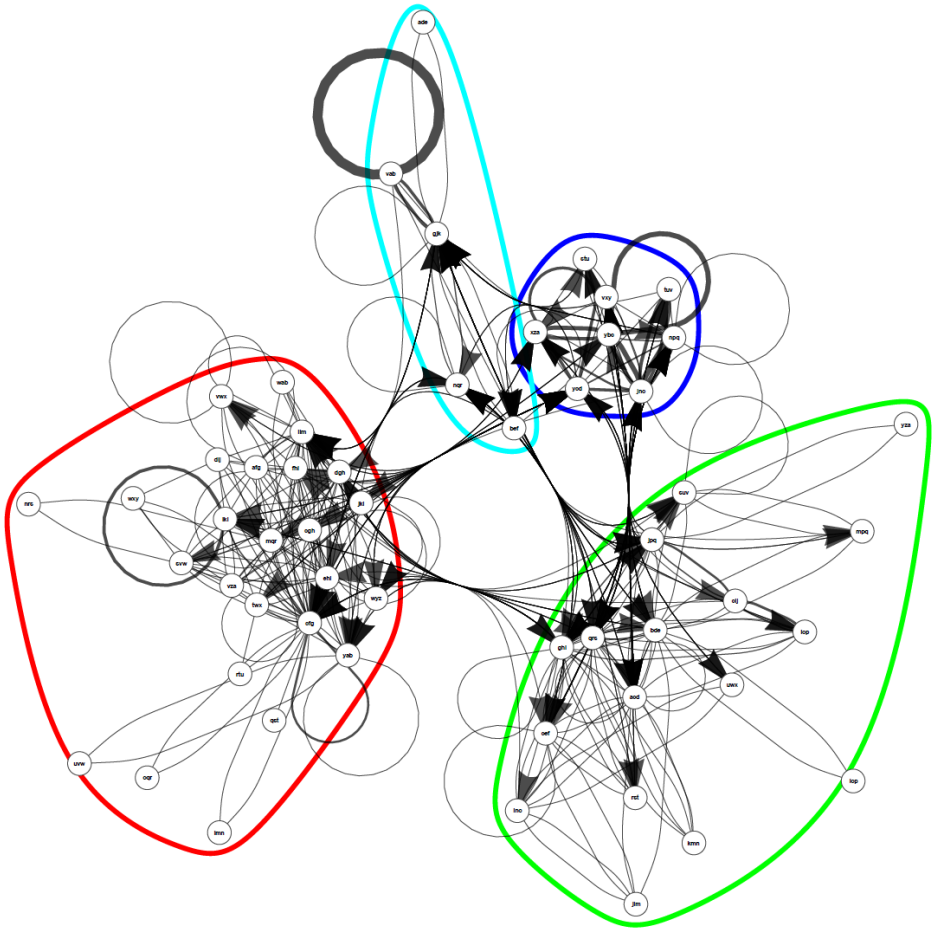
b)



c)

Figure A3.6 Network features for 2007 (S=1.2, N=4)

2008 Network features



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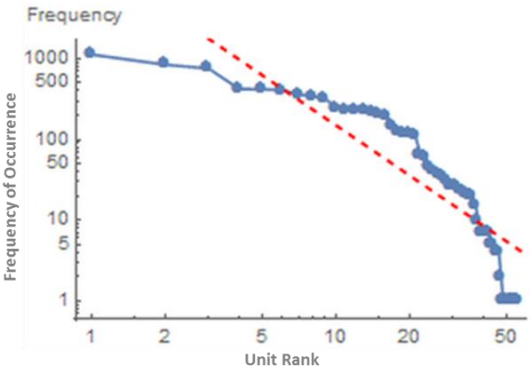

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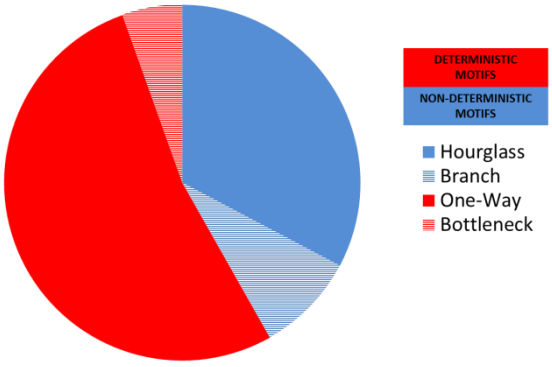
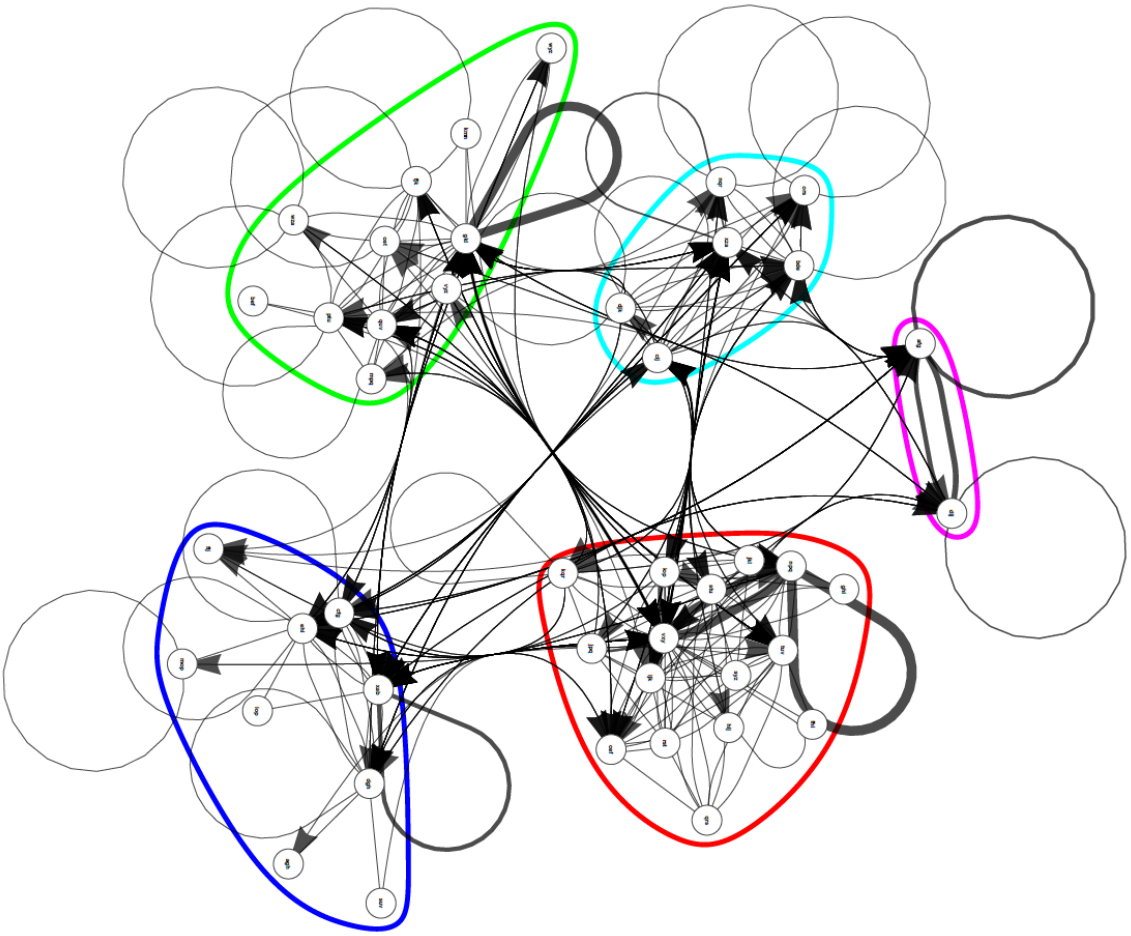


c)

Figure A3.7 Network features for 2008 (S=2.4, N=36)

2009 Network features



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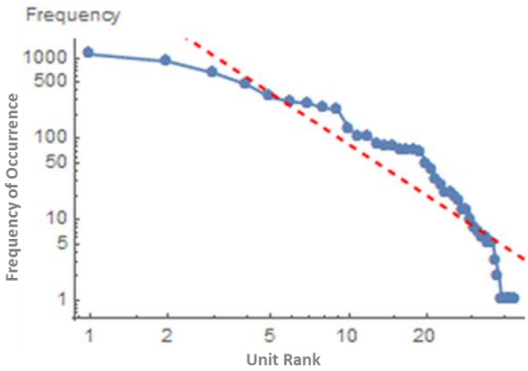

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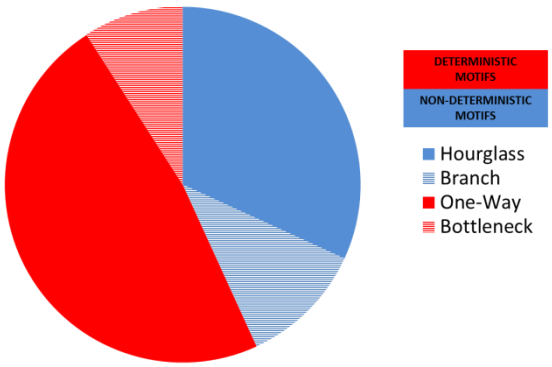
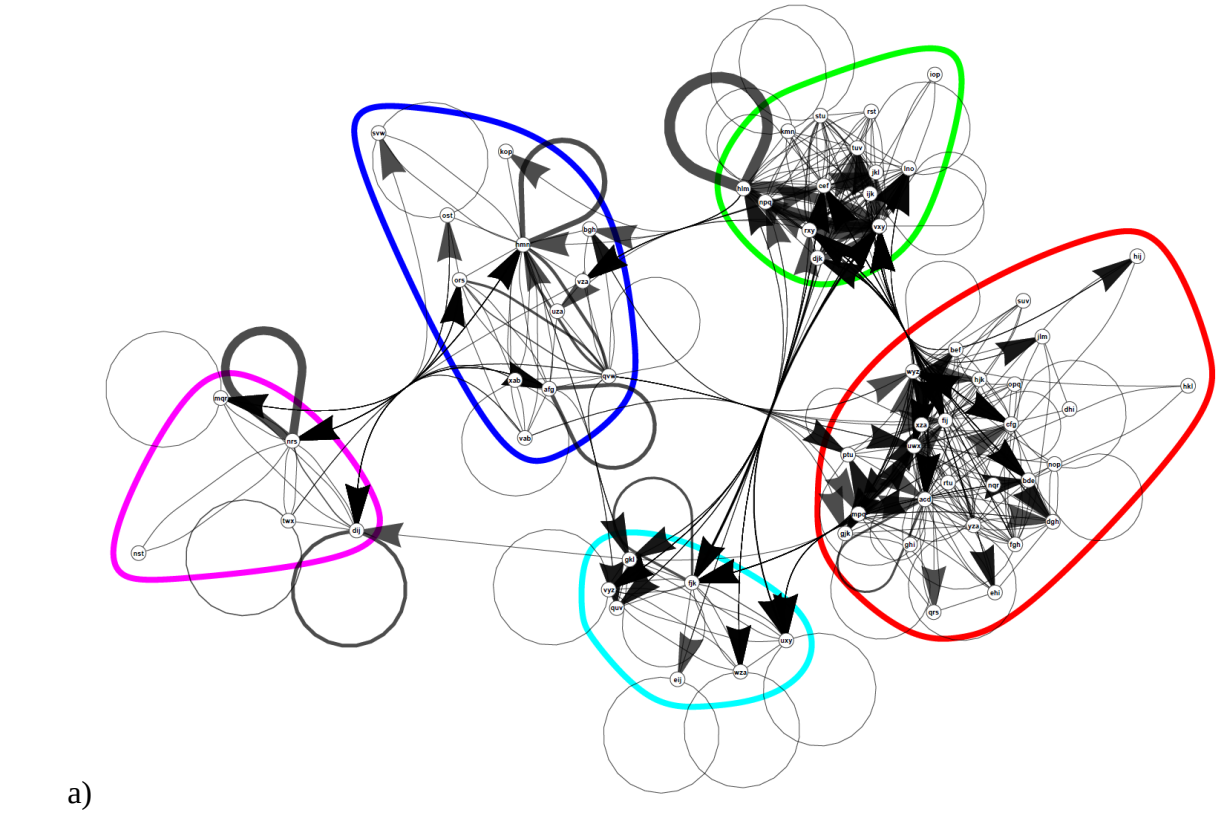


c)

Figure A3.8 Network features for 2009 (S=2.6, N=36)

2010 Network features



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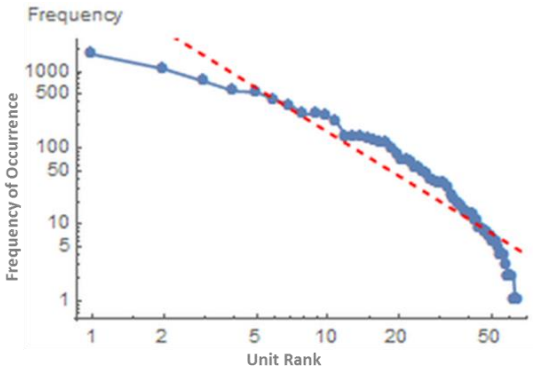

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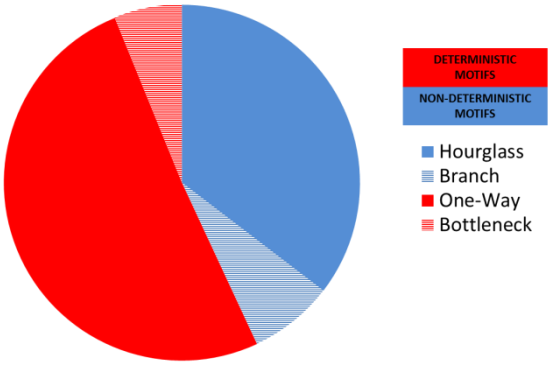
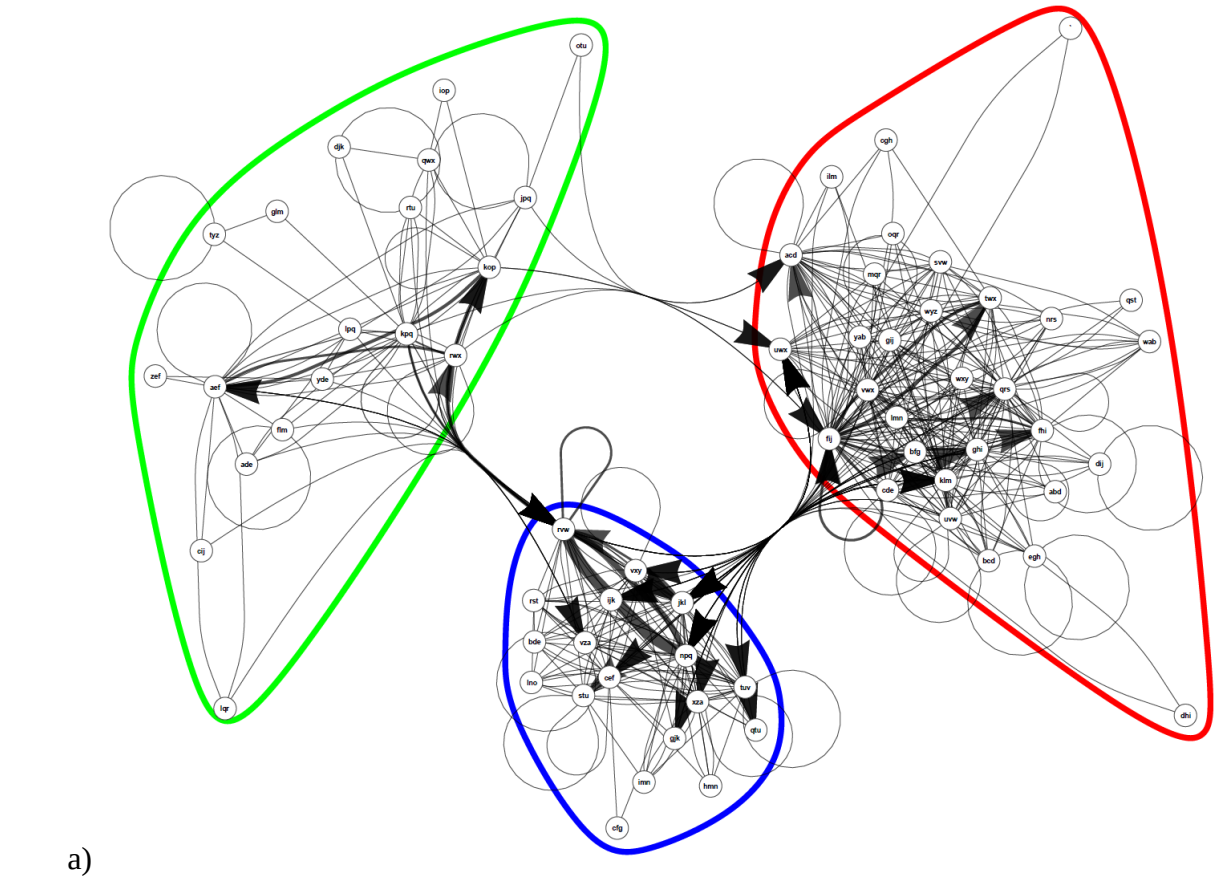


c)

Figure A3.9 Network features for 2010 (S=3.1, N=36)

2011 Network features



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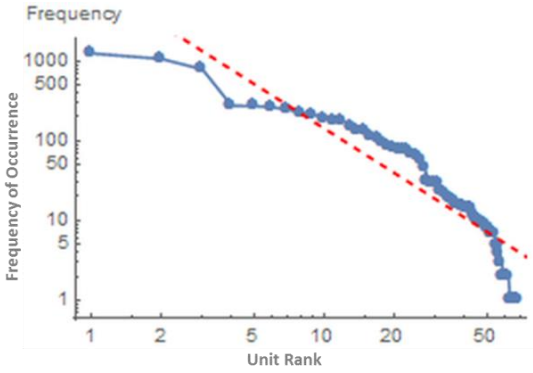

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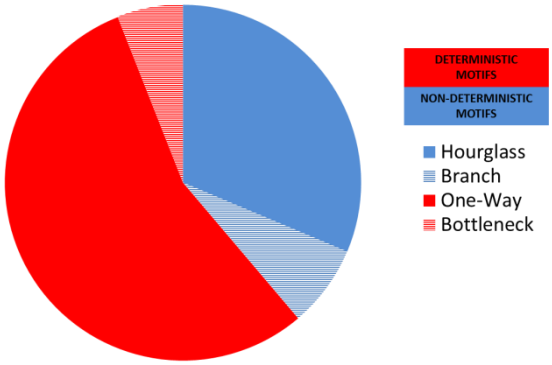
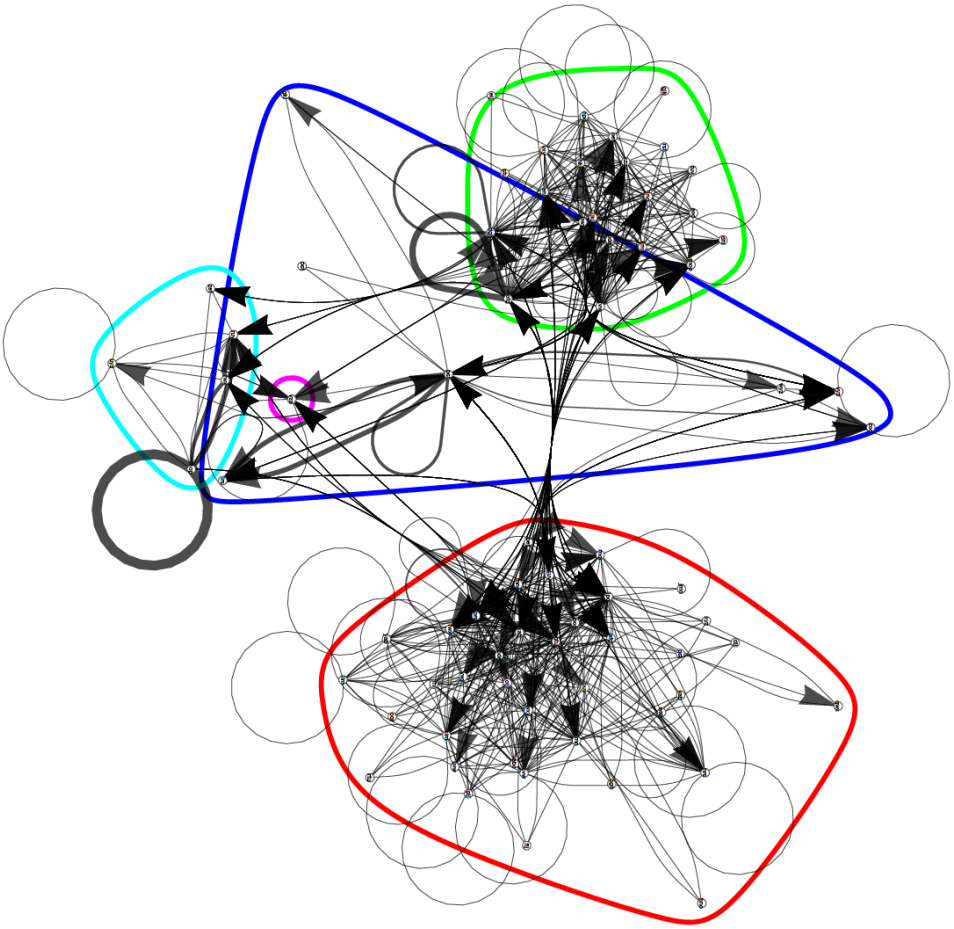


c)

Figure A3.10 Network features for 2011 (S=3.6, N=36)

2012 Network features



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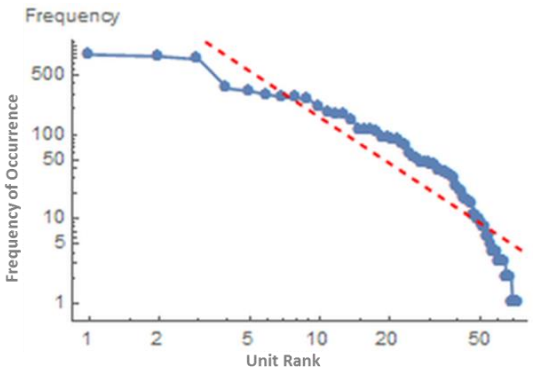

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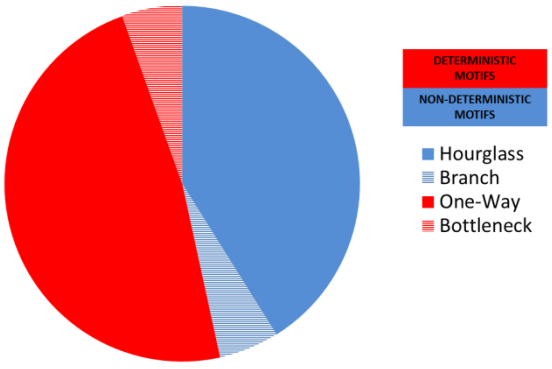
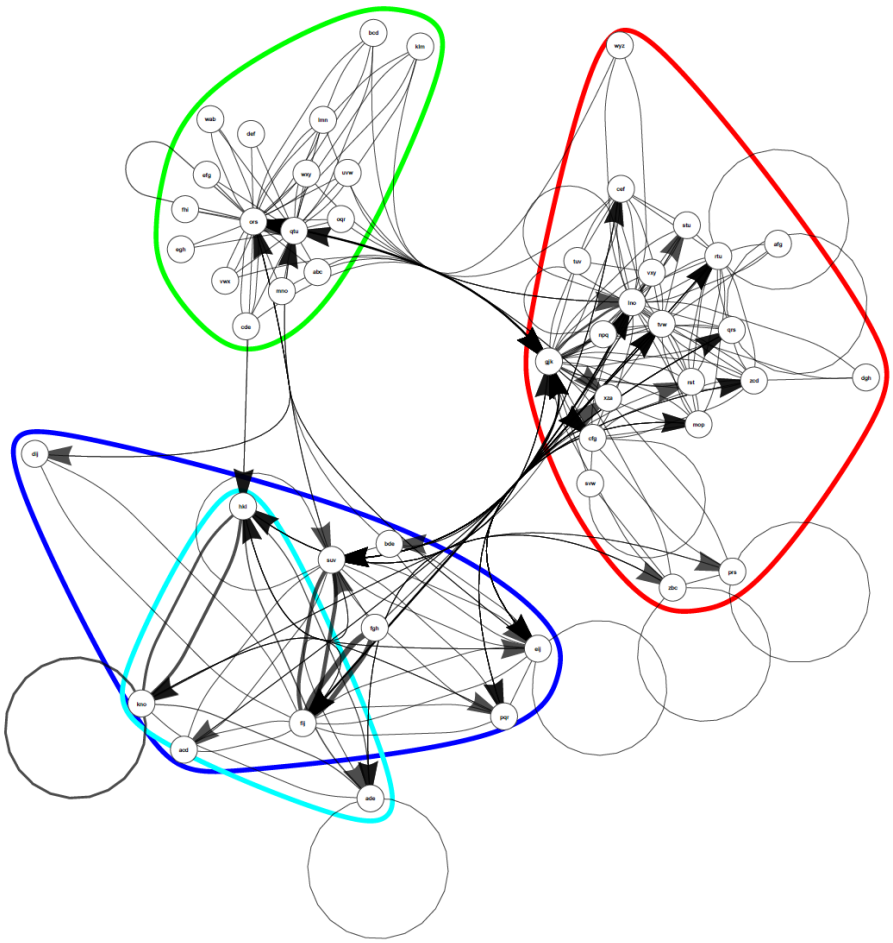


c)

Figure A3.11 Network features for 2012 (S=3.2, N=36)

2013 Network features



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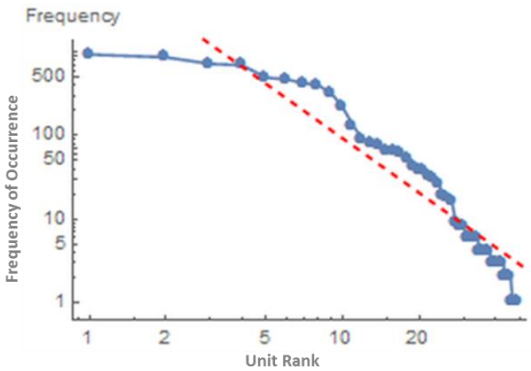

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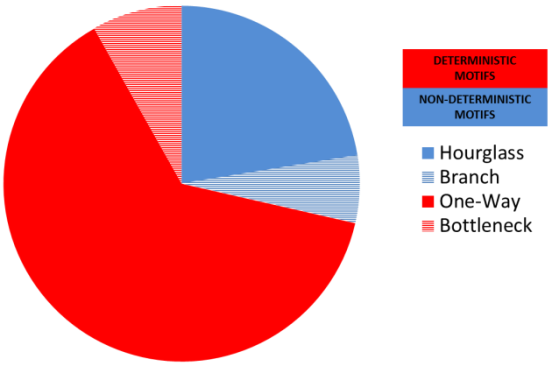
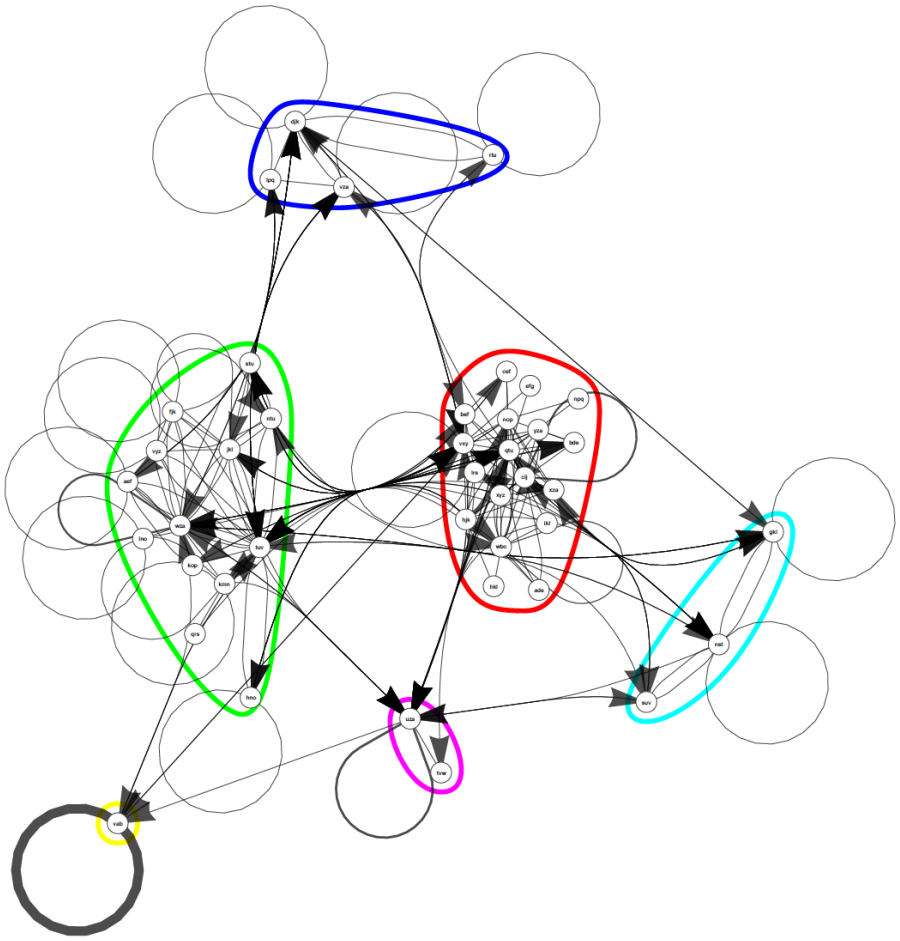


c)

Figure A3.12 Network features for 2013 (S=5.1, N=36)

2014 Network features



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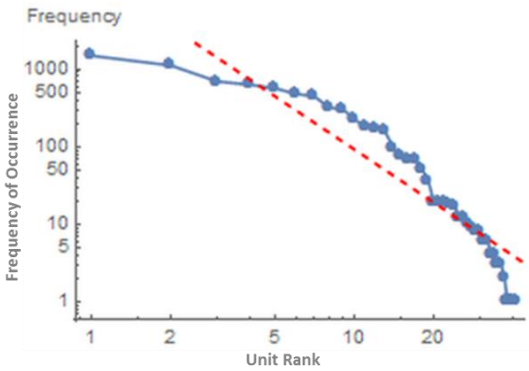

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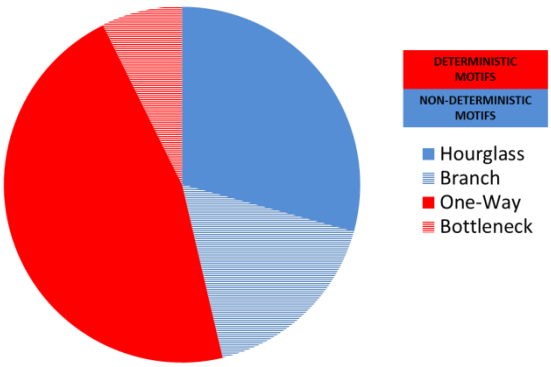
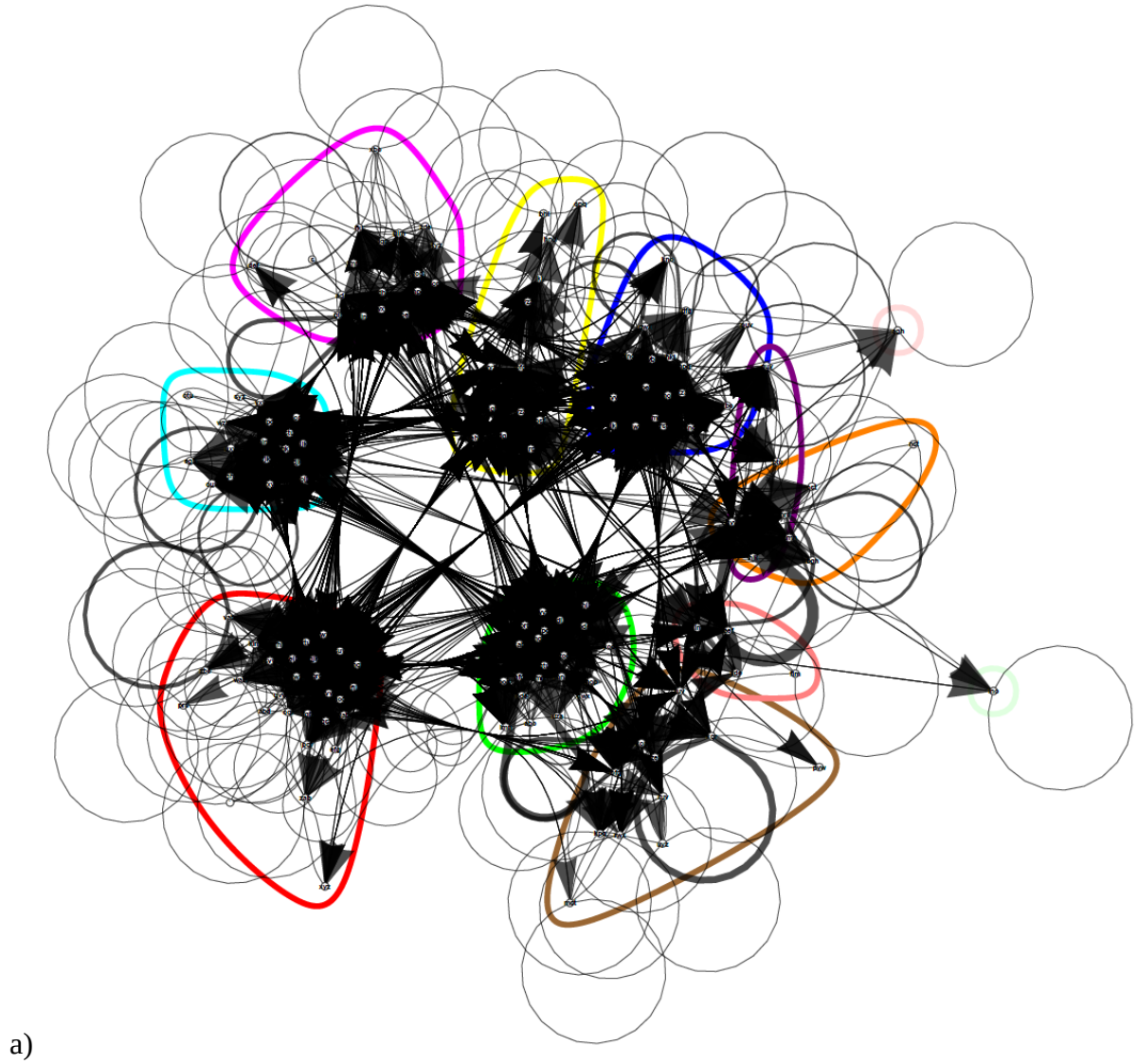


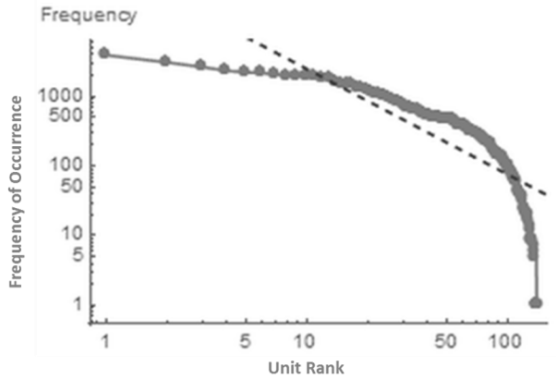
c)

Figure A3.13 Network features for 2014 (S=2.5, N=36)

All years network features



a)



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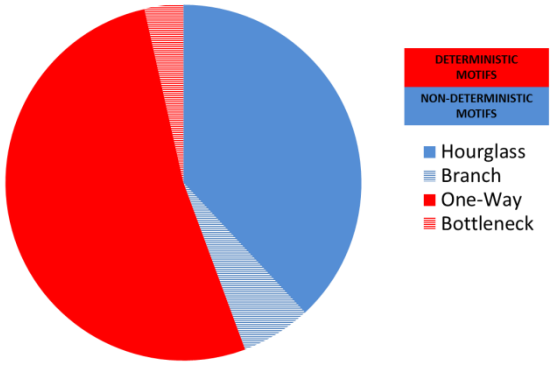

c)

Figure A3.14 Network features for all years combined (S=2.6, N=412)

Appendix 4: Song type spectrograms

Spectrograms are shown for each theme in each song type with time (s) on the x-axis and frequency (kHz) on the y-axis

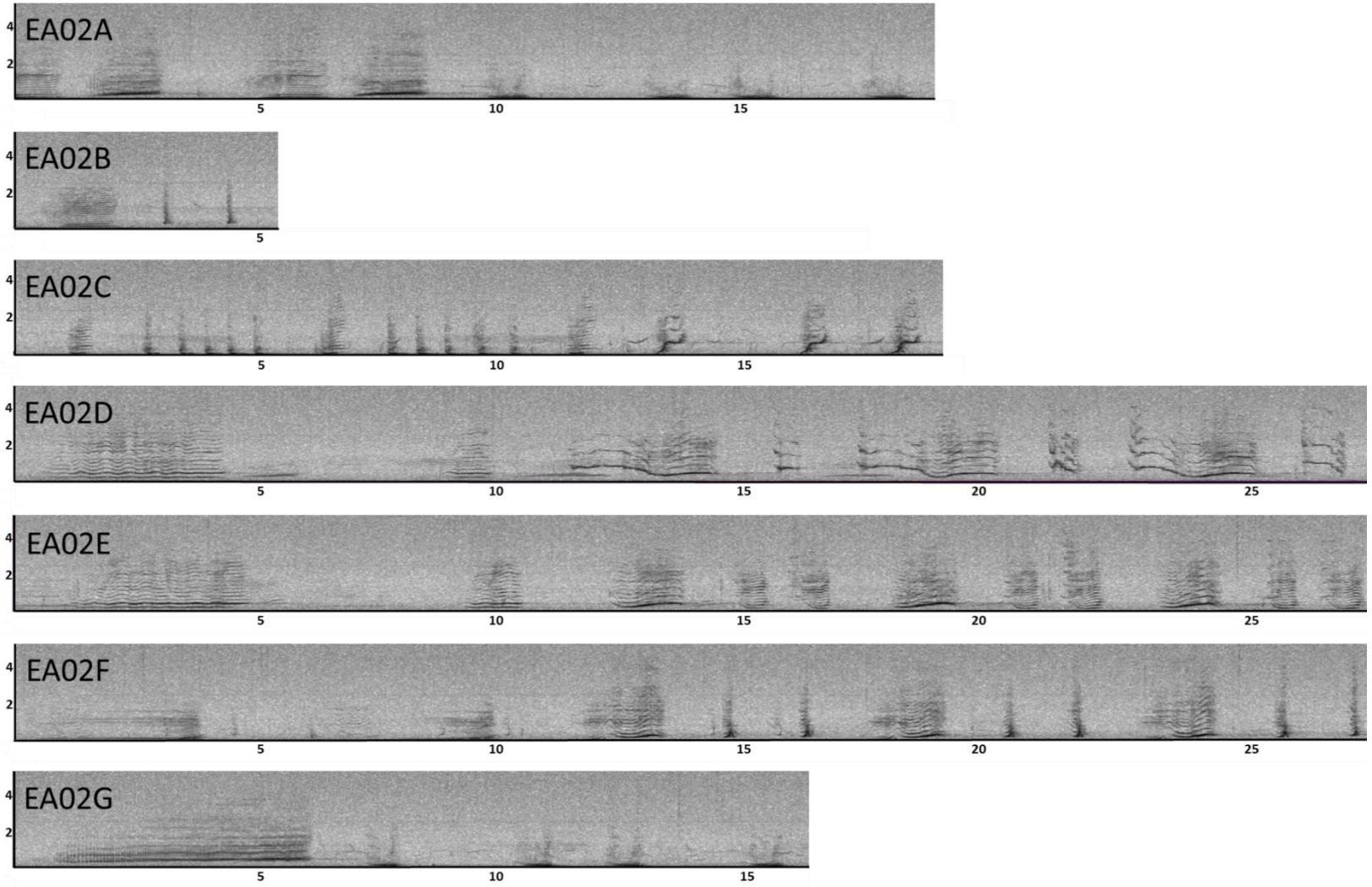

Figure A4.1 Blue song type from east Australia 2002

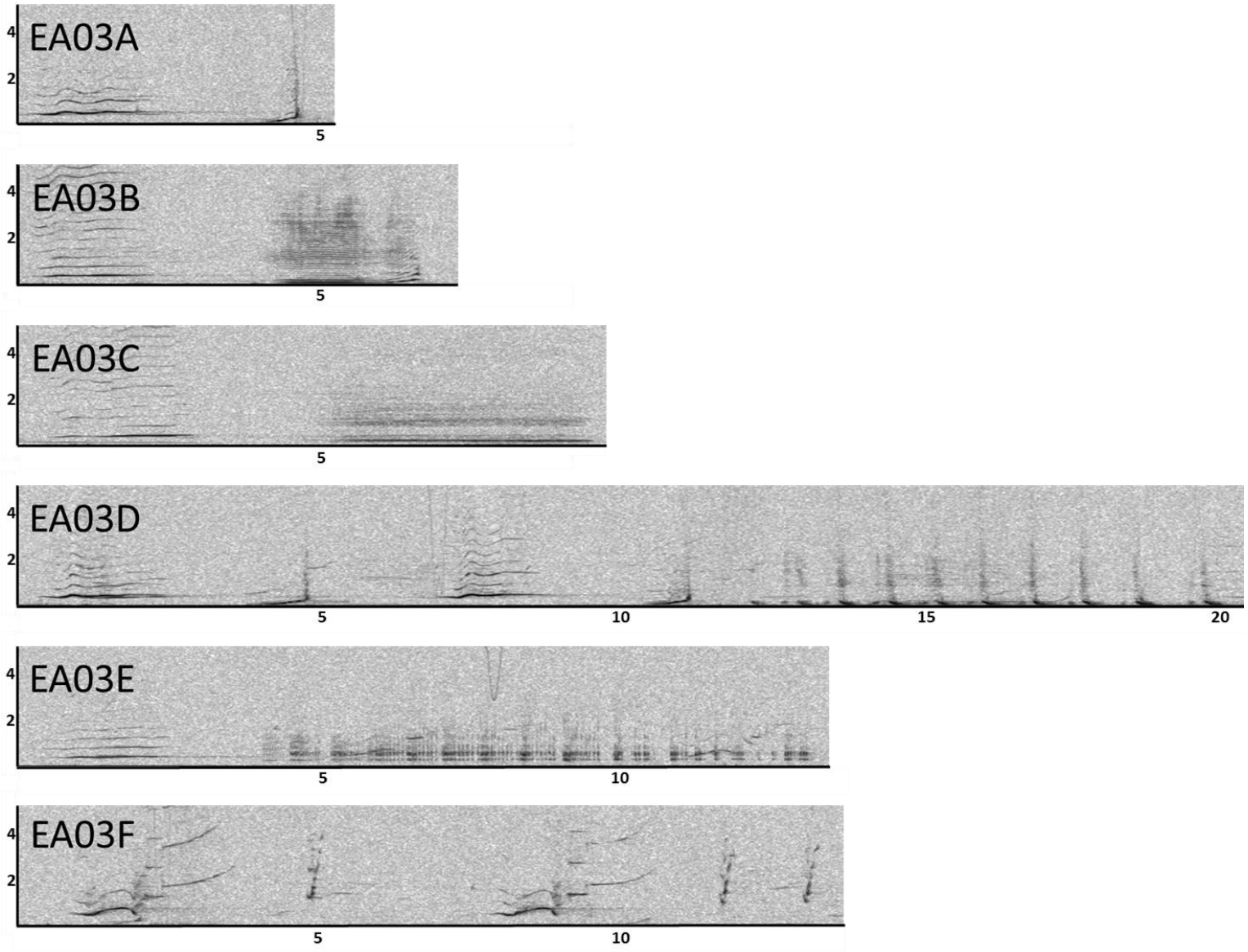

Figure A4.2 Dark Red song type from east Australia 2003

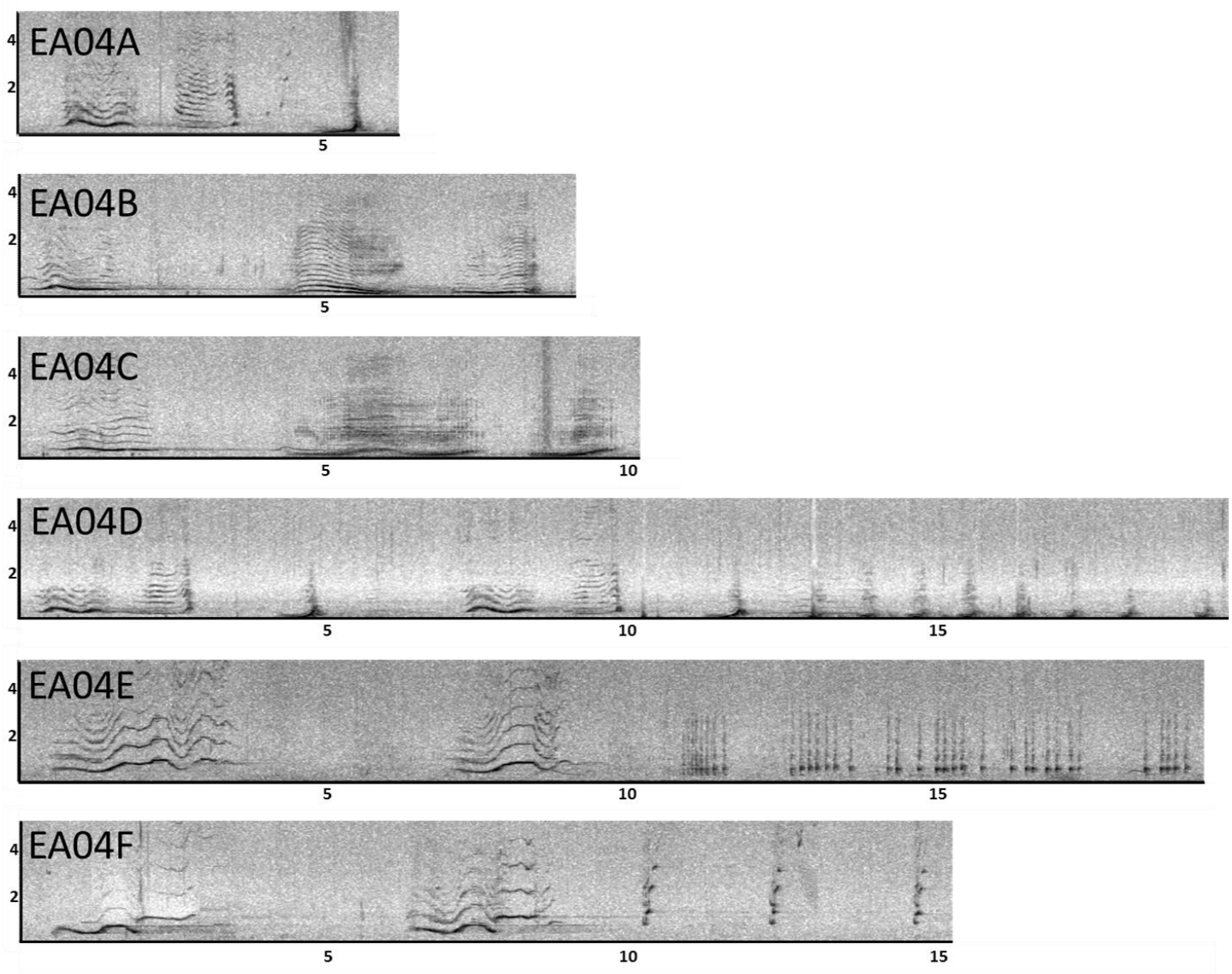

Figure A4.3 Red song type from east Australia 2004

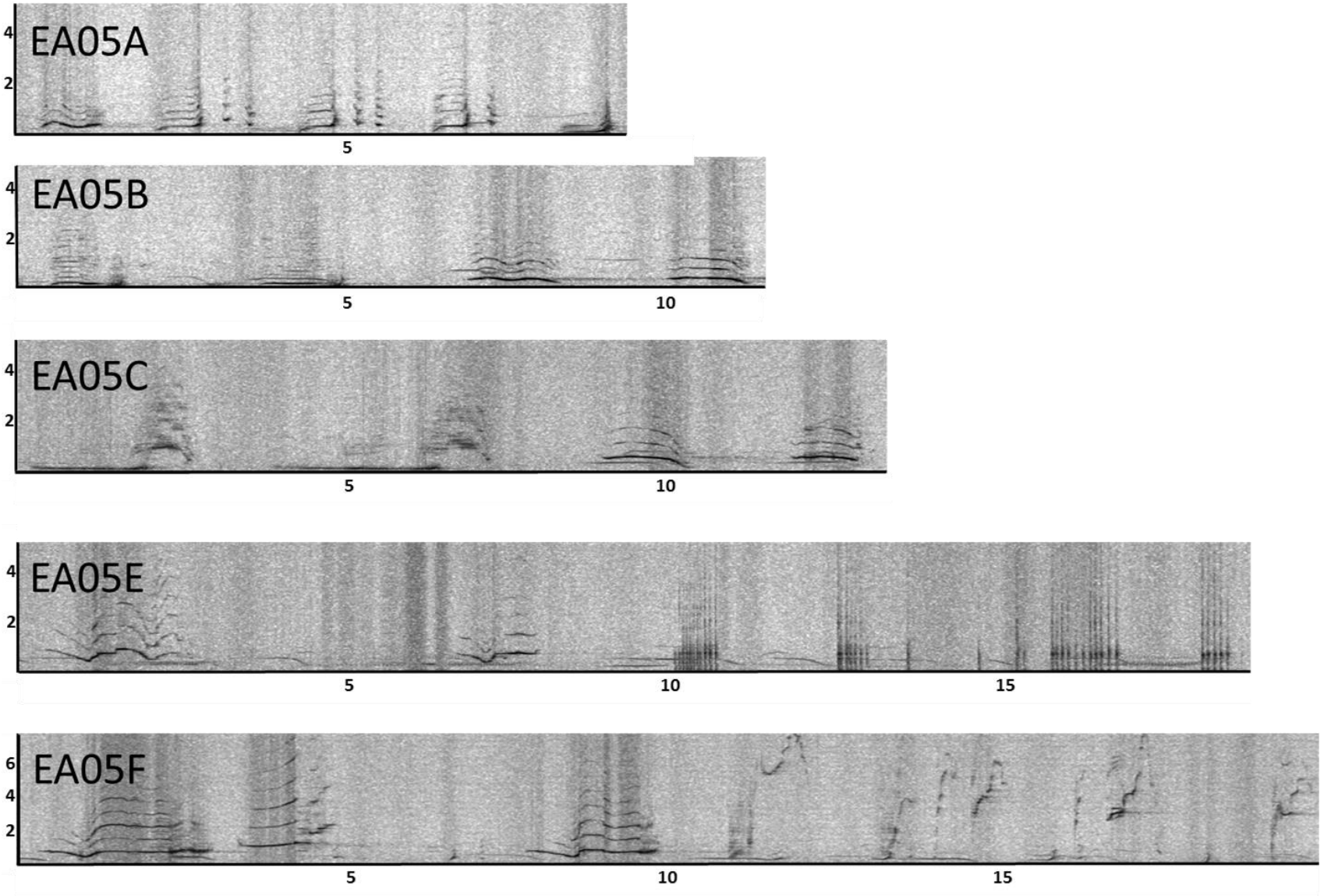

Figure A4.4 Light Red song type from east Australia 2005

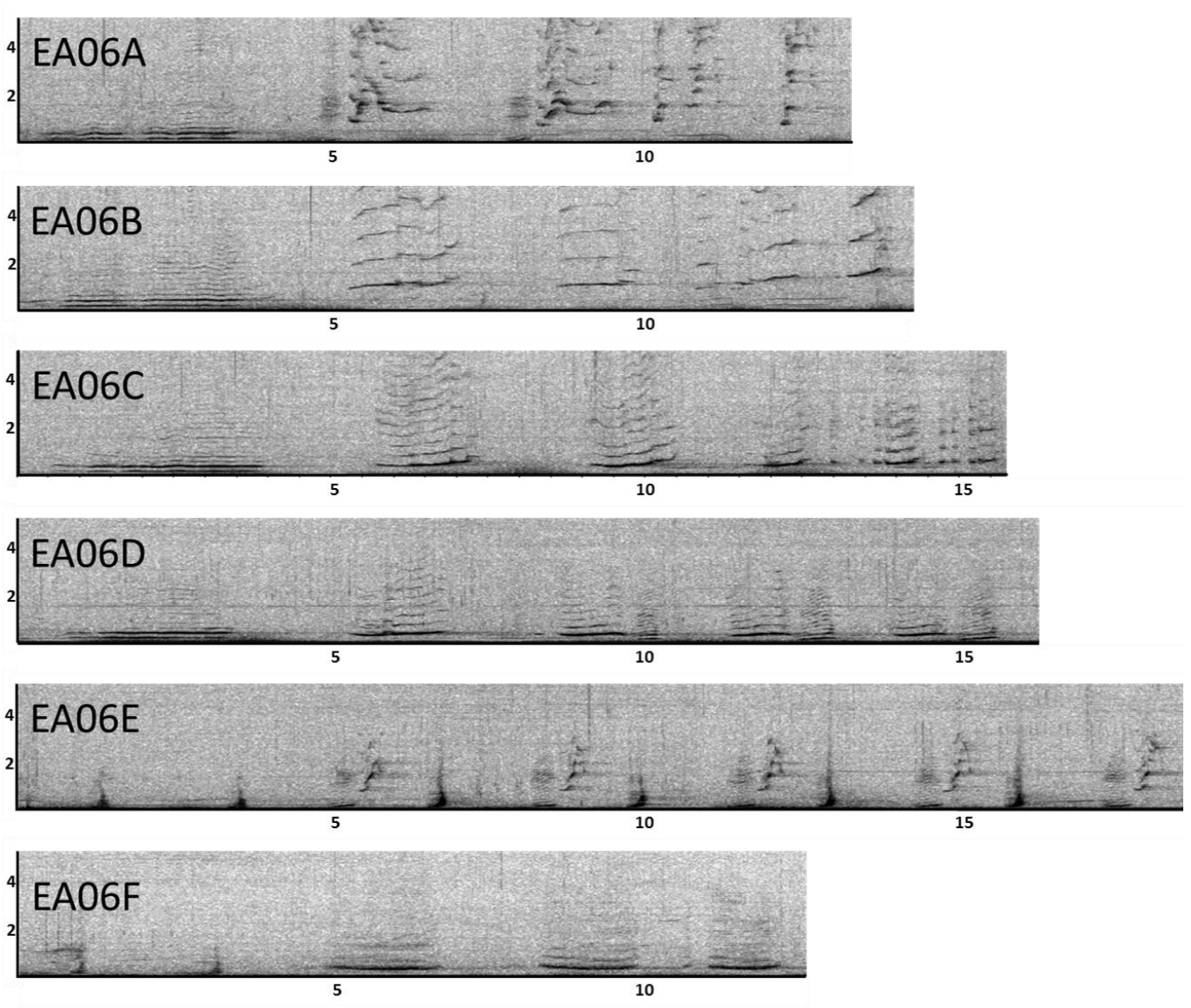

Figure A4.5 Yellow song type from east Australia 2006

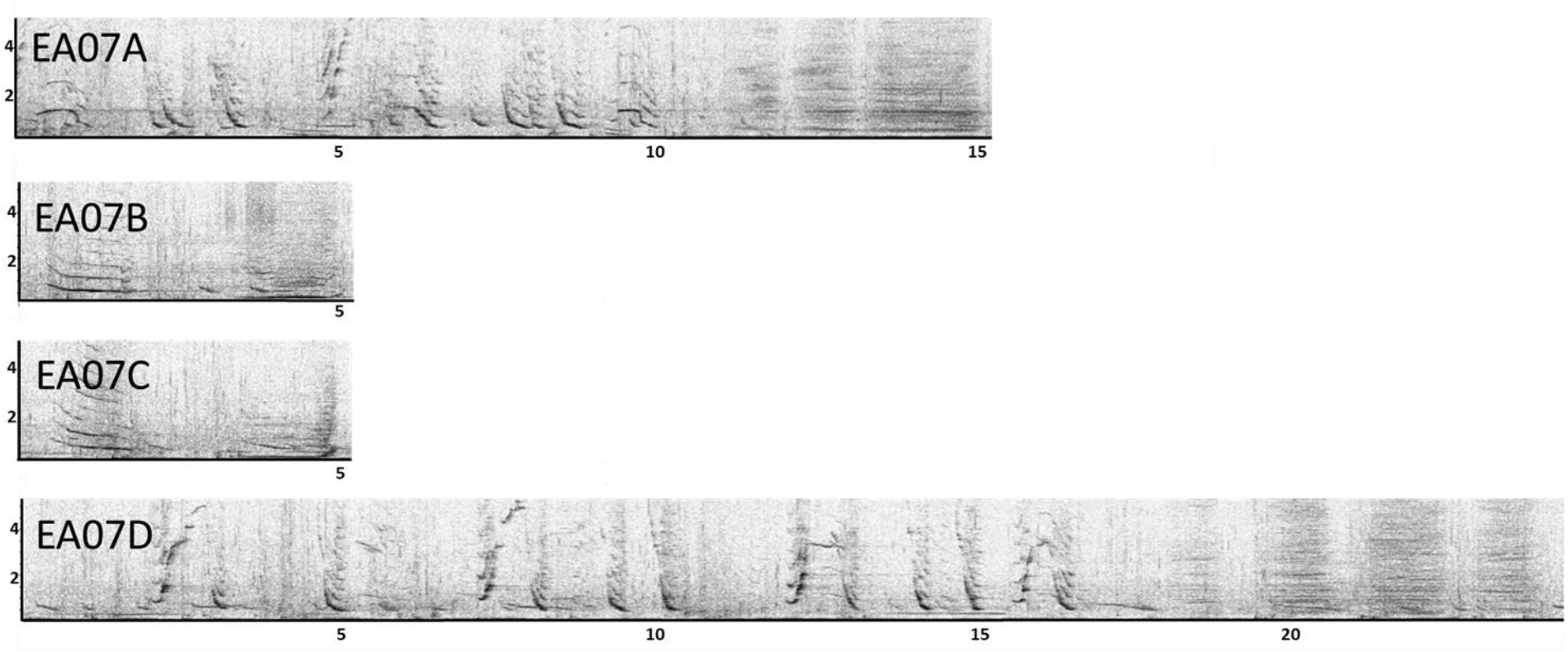

Figure A4.6 Dark Green song type from east Australia 2013

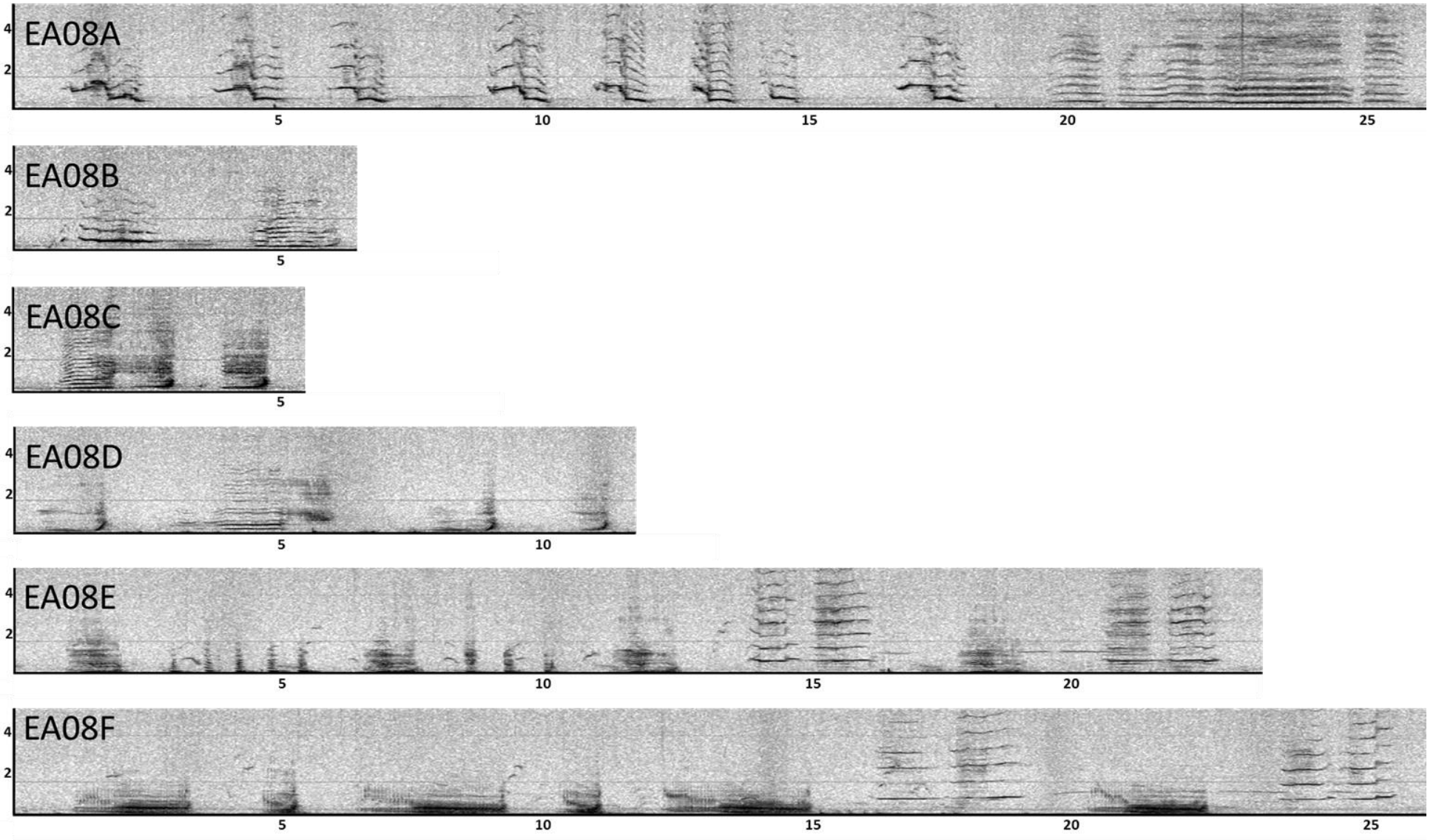

Figure A4.7 Light Green song type from east Australia 2008

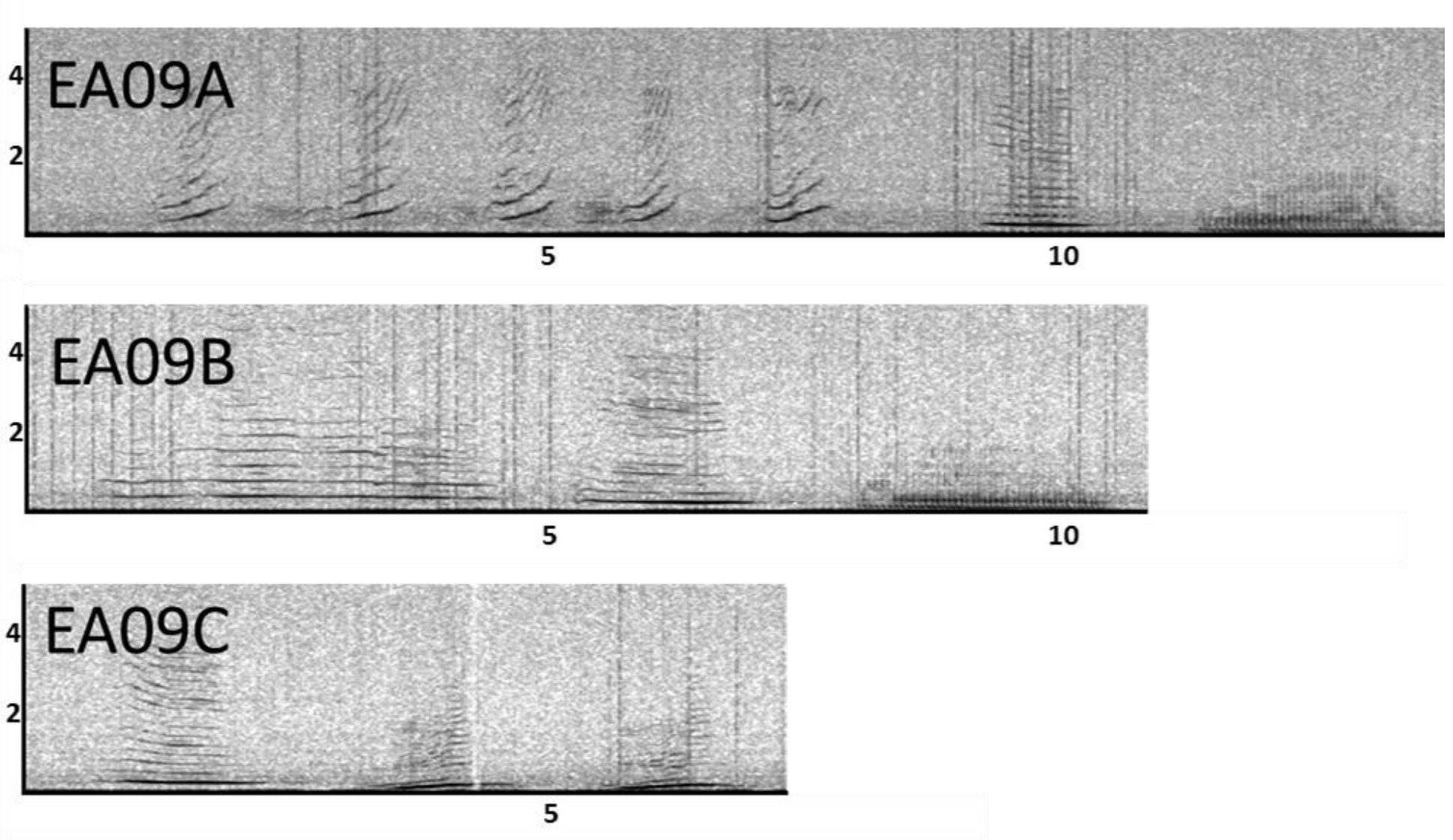

Figure A4.8 Dark Purple song type from east Australia 2009

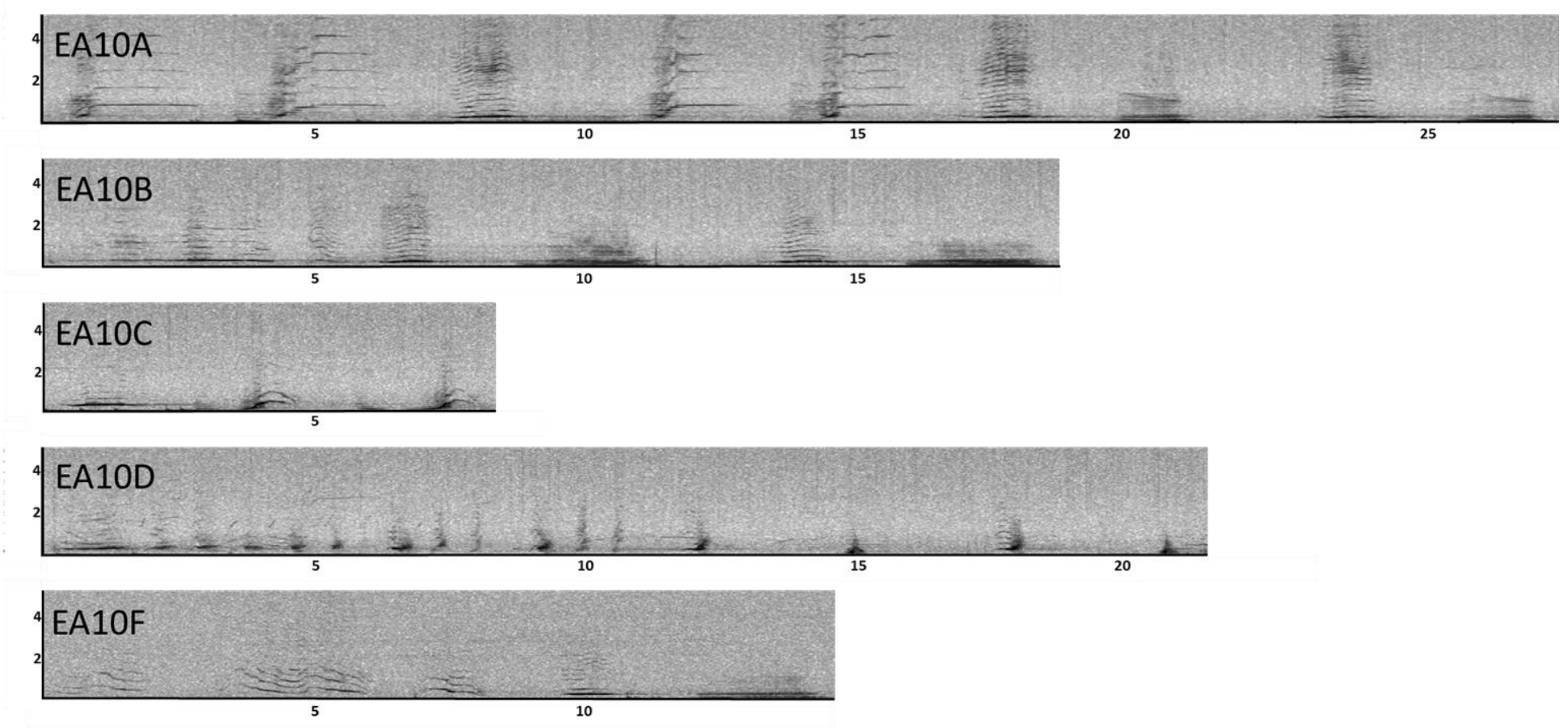

Figure A4.9 Light Purple song type from east Australia 2010

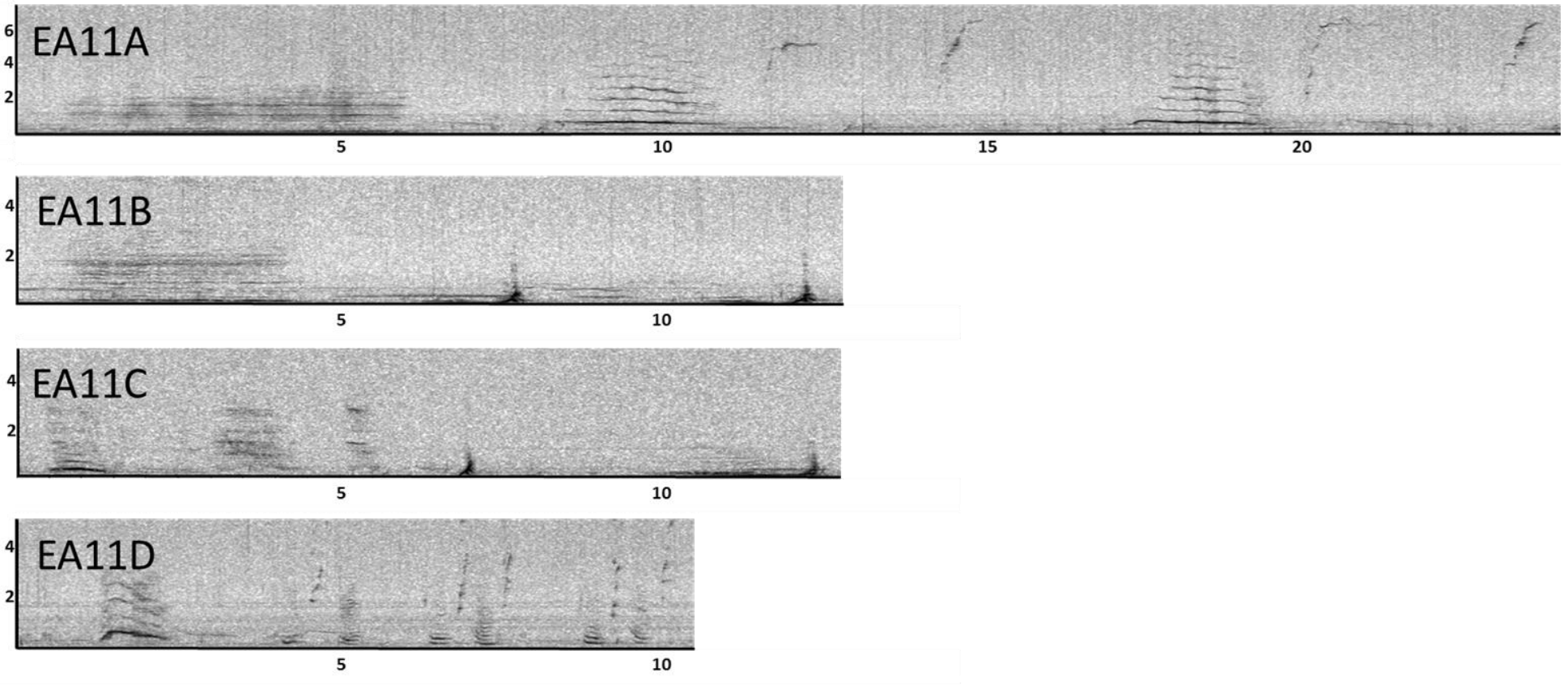

Figure A4.10 Dark Brown song type from east Australia 2011

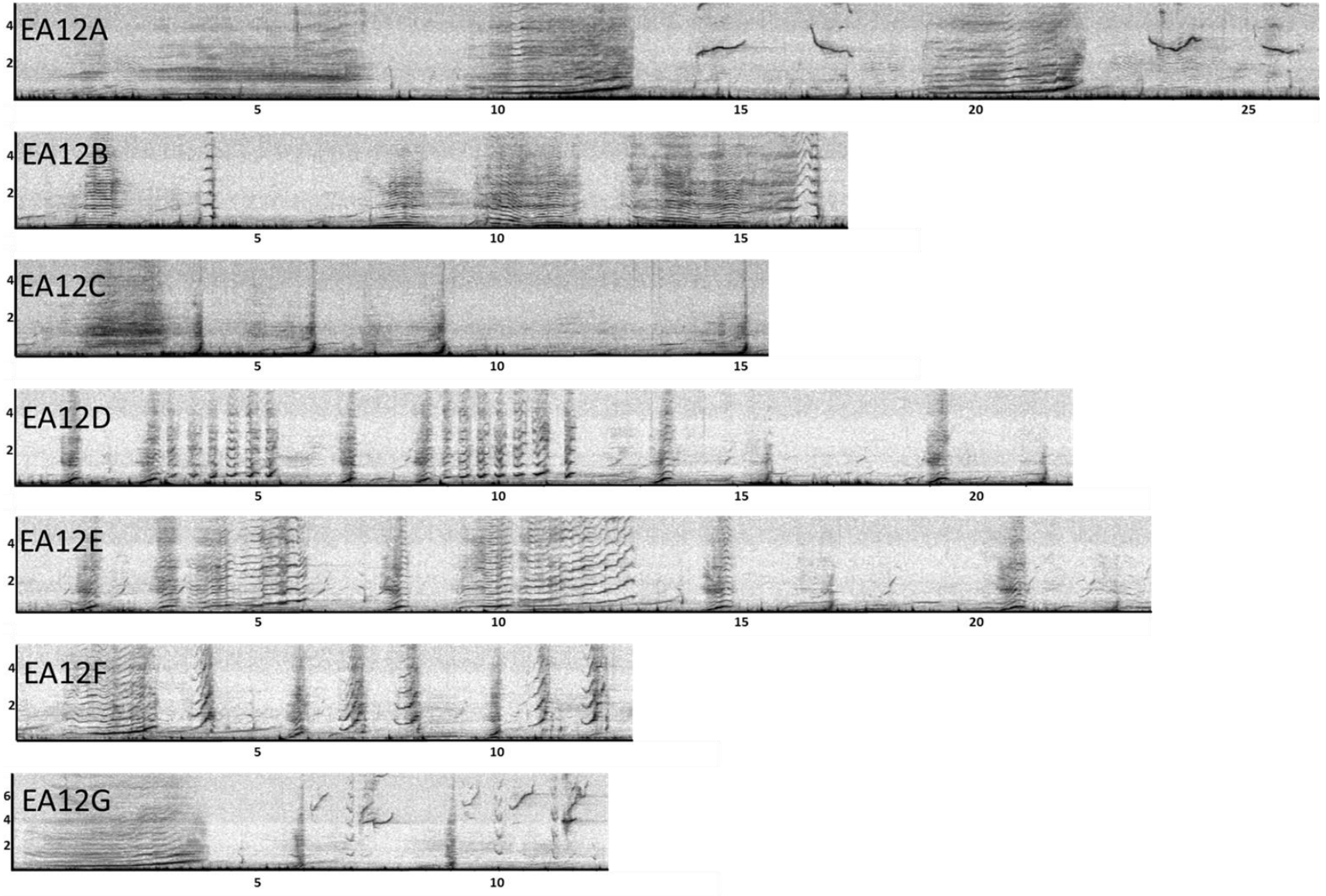

Figure A4.11 Light Brown song type from east Australia 2013

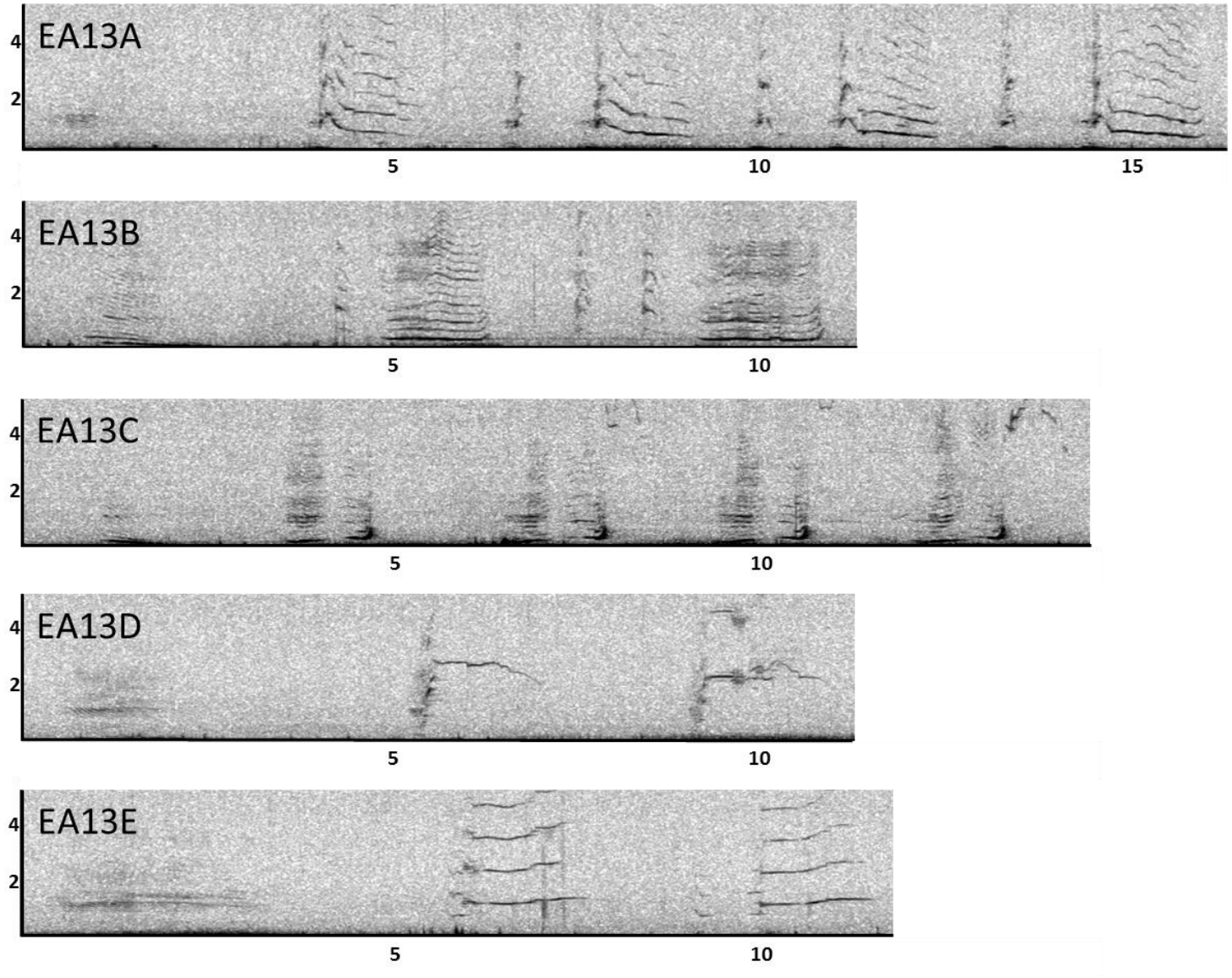

Figure A4.12 Teal song type from east Australia 2013

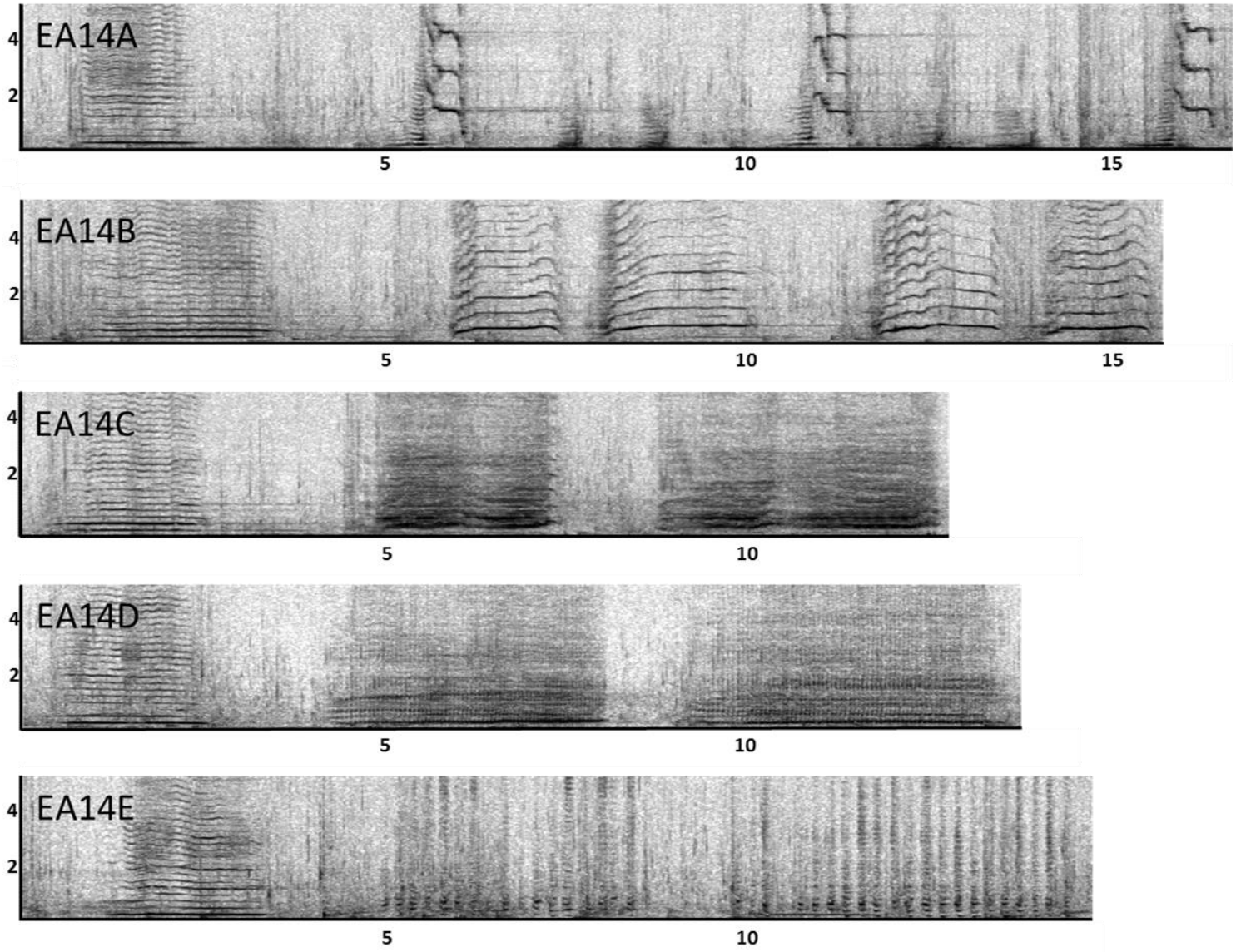

Figure A4.13 Orange song type from east Australia 2014

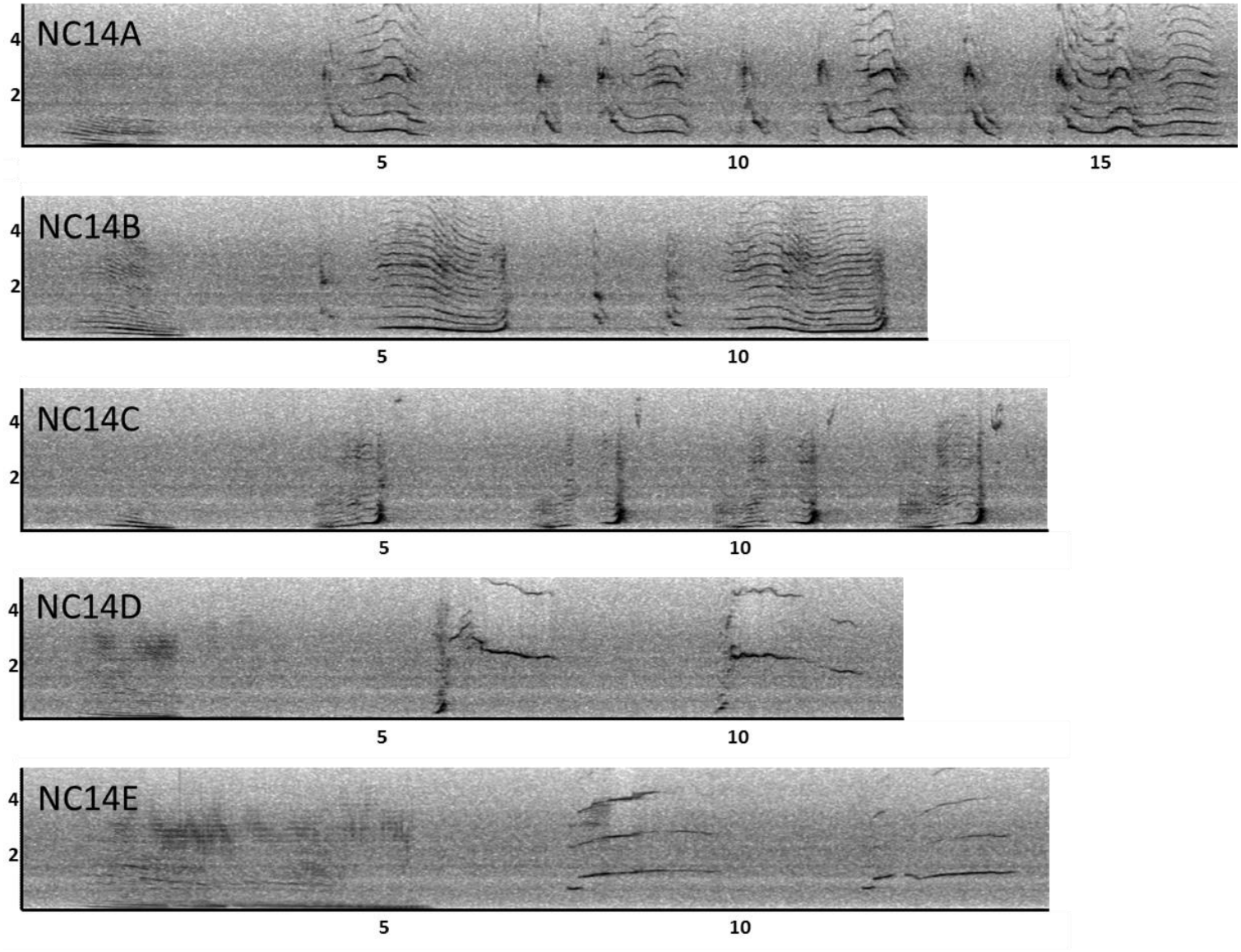

Figure A4.14 Teal song type from New Caledonia 2014

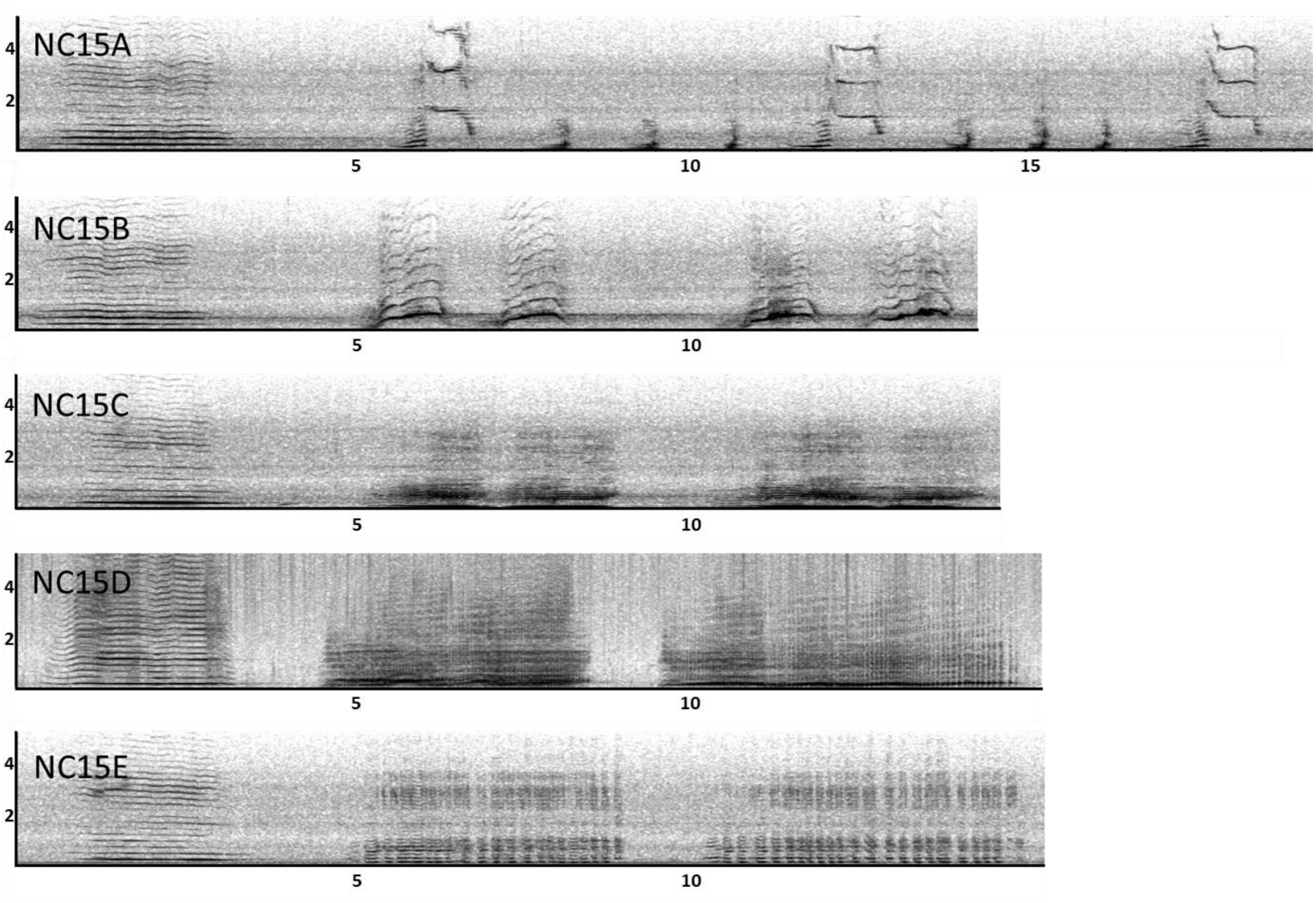

Figure A4.15 Orange song type from New Caledonia 2015

Appendix 5: Animal ethics approval certificates

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

Office of Research Ethics
Director
Nicole Shively

Animal Ethics Approval Certificate

25-Sep-2017

Please check all details below and inform the Animal Ethics Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Peter Hale
Title:	The Acoustic and Behavioural Ecology of Humpback Whales (Megaptera novaeangliae) During Migration
AEC Approval Number:	ZOO/ENT/250/02/USNR/DSTO
Previous AEC Number:	
Approval Duration:	13-Sep-2002 to 13-Sep-2003
Funding Body:	DSTO, USN
Group:	Molecular Biosciences
Other Staff/Students:	Michael Noad, D Paton, Damon Stokes, Hugh Possingham, Joanne Smith, G Deane, D Cato
Location(s):	

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins	Humpback Whales (Megaptera novaeangliae)	Other	Unknown	Other	100	4

Permits

Provisos

Approval Details

Description	Amount	Balance
Whales and Dolphins (Humpback Whales (Megaptera novaeangliae), Unknown, Other, Other)		
13 Sep 2002 Initial approval	100	100
31 Dec 2002 Annual Report 2002	-96	4

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THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

Office of Research Ethics
Director
Nicole Shively

Animal Ethics Approval Certificate

25-Sep-2017

Please check all details below and inform the Animal Ethics Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Peter Hale
Title:	The Acoustic and Behavioural Ecology of Humpback Whales (Megaptera novaeangliae) During Migration
AEC Approval Number:	ZOO/ENT/216/03/USNR/DSTO
Previous AEC Number:	ZOO/ENT/250/02/USNR/DSTO
Approval Duration:	02-Apr-2003 to 02-Apr-2004
Funding Body:	DSTO, USN
Group:	Molecular Biosciences
Other Staff/Students:	Michael Noad, D Paton, Damon Stokes, Hugh Possingham, Joanne Smith, G Deane, D Cato
Location(s):	

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins	Humpback Whales (Megaptera novaeangliae)	Adults	Unknown	Natural Habitat	450	231

Permits

Provisos

The CI is to ensure that he complies with all permit constraints.

Approval Details

Description	Amount	Balance
Whales and Dolphins (Humpback Whales (Megaptera novaeangliae), Unknown, Adults, Natural Habitat)		
2 Apr 2003 Initial approval	450	450
31 Dec 2003 Annual Report 2003	-219	231

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THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

Office of Research Ethics
Director
Nicole Shively

Animal Ethics Approval Certificate

25-Sep-2017

Please check all details below and inform the Animal Ethics Unit within 10 working days if anything is incorrect.

Activity Details

Chief Investigator:	Associate Professor Michael Noad, Veterinary Science
Title:	The Acoustic and Behavioural Ecology of Humpback Whales (Megaptera novaeangliae) During Migration
AEC Approval Number:	ZOO/ENT/239/04/USNR/DSTO
Previous AEC Number:	ZOO/ENT/216/03/USNR/DSTO
Approval Duration:	20-Apr-2004 to 20-Apr-2005
Funding Body:	DSTO, USN
Group:	Molecular Biosciences
Other Staff/Students:	D Cato, Joanne Smith, Damon Stokes, Hugh Possingham, G Deane, D Paton
Location(s):	

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins	Humpback Whales (Megaptera novaeangliae)	Adults	Unknown	Natural Habitat	600	317

Permits

Provisos

The CI is to ensure that he complies with all permit constraints.

Approval Details

Description	Amount	Balance
Whales and Dolphins (Humpback Whales (Megaptera novaeangliae), Unknown, Adults, Natural Habitat)		
20 Apr 2004 Initial approval	600	600
31 Dec 2004 Annual Report 2004	-283	317

Please Note: This is the second annual renewal form for this project. If applying to continue this project next year, a new Application Form will need to be completed. Please refer to Section 3 of the enclosed document entitled "Policies concerning animal experimentation".

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THE UNIVERSITY OF QUEENSLAND

PLEASE KEEP THIS FORM IT IS YOUR RECORD OF YOUR AEC APPROVAL NUMBER

Ms Ann Higgins
Animal Welfare Coordinator
The Office of Research and Postgraduate Studies
Cumbrae-Stewart Building (72)
St Lucia Q 4072

Ph: (07) 3365 52713 Fax: (07) 3365 4455
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ANIMAL ETHICS APPROVAL CERTIFICATE

Dear Dr Michael Noad, School of Veterinary Science

The following project: *Recording humpback whale song*

Requesting funding from (Grant Awarding Body):- DSTO & US ONR involves animal experimentation. It has been reviewed and ethical clearance obtained from the University Animal Ethics Committee (Group 2).

AEC Approval Number: SVS/381/05/DSTO & US ONR

Previous AEC No:

Approval Duration: 30/06/2005 to 30/06/2006

Permit(s):

Species	Breed/Strain	Class	Source	Amount
Whales, Dolphi	Humpback Whales (Megaptera n	Adults & Juvenile	Natural Habitat	300

Proviso(s)

Please use this Approval Number:

1. When ordering animals from Animal Breeding Houses.
2. For labelling of all animal cages or holding areas. In addition please include on the label,Chief Investigator's name and contact phone number.
3. When you need to communicate with this office about the project.

It is a condition of this approval that all animal usage details be made available to Animal House OIC.
(UAEC Ruling 14/12/2001)

THE UNIVERSITY OF QUEENSLAND

Ms Ann Higgins
Animal Welfare Coordinator
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Cumbrae-Stewart Building (72)
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PLEASE KEEP THIS FORM IT IS YOUR RECORD OF YOUR AEC APPROVAL NUMBER

ANIMAL ETHICS APPROVAL CERTIFICATE

Dear Dr Michael Noad, School of Veterinary Science

The following project: *Recording humpback whale song*

Requesting funding from (Grant Awarding Body):- DSTO & US ONR involves animal experimentation. It has been reviewed and ethical clearance obtained from the University Animal Ethics Committee (Group 4).

AEC Approval Number: SVS/870/06/DSTO & US ONR

Previous AEC No: 381/05

Approval Duration: 10/01/2006 to 10/01/2007

Permit(s): No permits required as there is no interference with the animals.

Species	Breed/Strain	Class	Source	Amount
Whales, Dolphi	Humpback Whales (Megaptera n	Adults & Juvenile	Natural Habitat	100

Proviso(s)

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ANIMAL ETHICS APPROVAL CERTIFICATE

Dear Dr Michael Noad, School of Veterinary Science

The following project: *Recording humpback whale song*

Requesting funding from (Grant Awarding Body):- DSTO & US ONR involves animal experimentation. It has been reviewed and ethical clearance obtained from the University Animal Ethics Committee (Group 4).

AEC Approval Number: SVS/203/07/DSTO & US ONR

Previous AEC No: 870/06

Approval Duration: 18/04/2007 to 18/04/2008

Permit(s): No permits required as there is no interference with the animals.

Species	Breed/Strain	Class	Source	Amount
Whales, Dolphi	Humpback Whales (Megaptera n	Adults & Juvenile	Natural Habitat	200

Proviso(s)

The CI must ensure that all appropriate permits required in other countries are obtained.

The CI must keep a logbook of sites visited in the South Pacific region, on what dates and the number of animals involved etc. for audit or committee inspection purposes.

Please use this Approval Number:

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ANIMAL ETHICS APPROVAL CERTIFICATE

Date: 28-Apr-2008

Dear Dr Michael Noad, Veterinary Science

The following project: *Humpback whales and the impact of noise: Controlled exposure experiments*

Requesting funding from (Grant Awarding Body):- ACAMMS involves animal experimentation. It has been reviewed and ethical clearance obtained from the University Animal Ethics Committee (Native and exotic wildlife and marine animals).

AEC Approval Number: SVS/299/08/ACAMMS

Previous AEC Number:

Approval Duration: 01-Jul-2008 to 01-Jul-2009

Permit(s):

SUBSPECIES	STRAIN	CLASS	SOURCE	Amount
Whales, Dolphins and Dugongs	Humpback Whales (Megaptera novaeangliae)	Other	Natural Habitat	**1,000**

Proviso(s):

Please use this Approval Number:
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3. When you need to communicate with this office about the project.

It is a condition of this approval that all animal usage details be made available to Animal House OIC.
(UAEC Ruling 14/12/2001)

This certificate supercedes all preceeding certificates for this project (i.e. those certificates dated before 28-Apr-2008

THE UNIVERSITY OF QUEENSLAND

PLEASE KEEP THIS FORM IT IS YOUR RECORD OF YOUR AEC APPROVAL NUMBER

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ANIMAL ETHICS APPROVAL CERTIFICATE

Date: 08-Sep-2010

Dear Dr Michael Noad, Veterinary Science

The following project: *Humpback whales and the impact of seismic exploration noise*

Requesting funding from (Grant Awarding Body):- involves animal experimentation. It has been reviewed and ethical clearance obtained from the University Animal Ethics Committee (Native and exotic wildlife and marine animals).

AEC Approval Number: SVS/230/10/(NF)

Previous AEC Number: SVS/283/09/

Approval Duration: 07-Sep-2010 to 07-Sep-2012

Permit(s):

Access to Biological Resources in a Commonwealth Area for Non-Commercial Purposes AU-COM2010082	26-Aug-2010 to 30-Jun-2011
Cetacean Permit 2010-0002	25-Aug-2010 to 30-Jun-2011
Scientific Purposes Permit WISP07966310	13-Sep-2010 to 30-Jun-2011

SUBSPECIES	STRAIN	CLASS	GENDER	SOURCE	AMOUNT
Whales and Dolphins	Humpback Whales (Megaptera novaeangliae)	Other	Mix	Natural Habitat	2,500

Proviso(s):

The CI is required to keep a logbook of all volunteers who will be participating in this protocol, with this information provided to the AEC as required.

Please use this Approval Number:

1. When ordering animals from Animal Breeding Houses
2. For labelling of all animal cages or holding areas. In addition please include on the label, Chief Investigator's name and contact phone number.
3. When you need to communicate with this office about the project.

It is a condition of this approval that all animal usage details be made available to Animal House OIC. (UAEC Ruling 14/12/2001)

This certificate supercedes all preceeding certificates for this project (i.e. those certificates dated before 08-Sep-2010

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UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

ANIMAL ETHICS APPROVAL CERTIFICATE

20-Sep-2012

Activity Details

Chief Investigator:	Dr Michael Noad, Veterinary Science
Title:	Humpback whales and the impact of seismic exploration noise
AEC Approval Number:	SVS/403/12/EPSML
Previous AEC Number:	SVS/230/10/(NF)
Approval Duration:	21-Sep-2012 to 21-Sep-2013
Funding Body:	
Group:	Native and exotic wildlife and marine animals
Other Staff/Students:	Rebecca Dunlop, Sasha Collecutt, David Paton, Robert Slade, Verity Steptoe, Michael Williamson
Location(s):	Other Queensland Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins	Humpback Whales (Megaptera novaeangliae)	Adults	Mix	Natural Habitat	60	60

Permit(s):

Scientific Purposes Permit WITK09644911	7/19/2011 to 12/31/2013
Scientific Purposes Permit WISP09645411	8/1/2011 to 12/31/2013

Proviso(s):

The CI is required to keep a logbook of all volunteers who will be participating in this protocol, with this information provided to the AEC as required.

Approval Details

Description	Amount	Balance
Whales and Dolphins (Humpback Whales (Megaptera novaeangliae), Mix, Adults, Natural Habitat)		
20 Sep 2012 Initial Approval	60	60

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ANIMAL ETHICS APPROVAL CERTIFICATE

20-Aug-2013

Activity Details

Chief Investigator:	Dr Michael Noad, Veterinary Science
Title:	Humpback whales and the impact of seismic exploration noise
AEC Approval Number:	CURTIN/SVS/283/13
Previous AEC Number:	
Approval Duration:	21-Aug-2013 to 21-Aug-2014
Funding Body:	
Group:	Native and exotic wildlife and marine animals
Other Staff/Students:	Rebecca Dunlop
Location(s):	Other Western Australian Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins		Other	Unknown	Other	0	0

Permit(s):

Proviso(s):

Animal numbers are not shown on this approval certificate, as the approved animal numbers are provided under AEC_2011_62 Curtin University AEC Approval.
This certificate is to show that the project has been ratified by a University of Queensland AEC.

Approval Details

Description	Amount	Balance
Whales and Dolphins (Unknown, Other, Other)		
13 Aug 2013 Ratification	0	0

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UQ Research and Innovation
Director, Research Management Office
Nicole Thompson

ANIMAL ETHICS APPROVAL CERTIFICATE

15-Apr-2014

Activity Details

Chief Investigator: Associate Professor Michael Noad, Veterinary Science

Title: ANRFA: Fine scale song exchange in two neighbouring populations of humpback whales.

AEC Approval Number: SVS/103/14

Previous AEC Number:

Approval Duration: 01-Jun-2014 to 01-Jun-2016

Funding Body:

Group: Native and exotic wildlife and marine animals

Other Staff/Students: Jennifer Allen, Rebecca Dunlop

Location(s): Other Queensland Location

Summary

Subspecies	Strain	Class	Gender	Source	Approved	Remaining
Whales and Dolphins		Adults	Mix	Natural Habitat	0	0

Permit(s):

Proviso(s):

· Animal numbers are not shown on this certificate as the animals did not die or where interfered with for the purposes of this project.

Approval Details

Description	Amount	Balance
Whales and Dolphins (Mix, Adults, Natural Habitat)		
8 Apr 2014 ANRFA	0	0

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